Vol. 36. Parts 7–9. Pp. 89–132. 21 figs. 30th September, 1961

THE PROCEEDINGS
OF THE
ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Series A

GENERAL ENTOMOLOGY

World List abbreviation : *Proc. R. ent. Soc. Lond.* (A)

CONTENTS

	PAGE
LEWIS, TREVOR. Records of THYSANOPTERA at Silwood Park, with notes on their biology .	89–95
WALOFF, N. Observations on the biology of *Perilitus dubius* (Wesmael) (HYMENOPTERA : BRACONIDAE), a parasite of the chrysomelid beetle *Phytodecta olivacea* (Förster) . .	96–102, 1 fig.
ASKEW, R. R. The biology of the British species of the genus *Olynx* Förster (HYMENOPTERA : EULOPHIDAE), with a note on seasonal colour forms in the CHALCIDOIDEA	103–112, 8 figs.
CORBET, PHILIP S. and HADDOW, A. J. Observations on nocturnal flight activity in some African CULICIDAE (DIPTERA) . . .	113–118, 2 figs.
POPHAM, E. J. The function of Hagemann's organ in *Corixa punctata* (Illig.) (HEMIPTERA : CORIXIDAE)	119–125, 6 figs.
MILNE, D. L. The function of the sternal spatula in gall midges	126–131, 4 figs.
BOOK NOTICE	132

LONDON
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.

Price 14s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded 1833. Incorporated by Royal Charter 1885

Patron:

HER MAJESTY THE QUEEN

OFFICERS AND COUNCIL FOR THE SESSION, 1961–1962

Professor G. C. Varley, *President*
Mr. R. B. Benson, *Vice-President*
Dr. N. E. Hickin, *Vice-President*
Mr. M. J. Way, *Vice-President*
Dr. C. G. Butler, *Treasurer*
Dr. Paul Freeman, *Secretary*
Mr. W. H. Potts, *Editor*

Other Members of Council

Professor D. S. Bertram
Dr. M. I. Crichton
Dr. K. U. Clarke
Mr. R. G. Davies
Dr. A. M. Easton
Dr. J. E. Harker
Dr. P. T. Haskell
Dr. B. R. Laurence
Mr. H. Oldroyd
Sir Boris Uvarov, K.C.M.G., F.R.S.

Miss E. Evans, *Registrar*

Finance and House Committee

Professor D. S. Bertram (*Chairman*)

Mr. J. P. Doncaster
Dr. J. A. Freeman, O.B.E.
Dr. N. E. Hickin
Dr. D. J. Lewis
Dr. M. E. Solomon

Publication and Library Committee

Mr. R. G. Davies (*Chairman*)

Dr. J. D. Carthy
Dr. P. T. Haskell
Dr. C. G. Johnson
Mr. D. Leatherdale
Mr. G. E. J. Nixon

Conservation (Insect Preservation) Committee

Mr. R. B. Benson (*Chairman*)

Dr. B. M. Hobby
Mr. T. G. Howarth
Dr. A. M. Massee
Mr. F. T. Vallins
Mr. M. J. Way

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society).
   Dr. H. E. Hinton, F.R.S., appointed 1958.
2. **Local Committee of Management of Wicken Fen.**
   Dr. John Smart, appointed 1960.
3. **National Trust for Places of Historic Interest or Natural Beauty.**
   Mr. N. D. Riley, C.B.E., appointed 1955.
4. **New Forest Association.**
   Mr. C. W. Mackworth-Praed, appointed 1948.
5. **New Forest Joint Committee.**
   Lt.-Col. F. C. Fraser, appointed 1949.
6. **Field Studies Council.**
   Dr. W. H. Thorpe, F.R.S., appointed 1944.
7. **Yorkshire Naturalists' Trust, Ltd.**
8. **The Biological Council.**
   Dr. N. E. Hickin, appointed 1952.
9. **The Parliamentary and Scientific Committee.**
   Dr. N. E. Hickin, appointed 1953.
10. **British Co-ordinating Committee for Nature Conservation**
    Mr. R. B. Benson, appointed 1960.
11. **Council for Nature.**
    Dr. N. E. Hickin, appointed 1958.

RECORDS OF THYSANOPTERA AT SILWOOD PARK, WITH NOTES ON THEIR BIOLOGY

By Trevor Lewis
(*School of Agriculture, Cambridge*)

Previous records of Thysanoptera in Berkshire (Morison, 1947–49; Smith, 1957) were confined principally to specimens taken on vegetation. In order to understand clearly the complete life cycle of many species more flight records are needed.

From 1956 to 1958 Thysanoptera were trapped at the Imperial College Field Station, Silwood Park, Berks., white water traps (Lewis, 1959) and suction traps (Taylor, 1951) being used. The traps were situated in a three-acre wheat field, bordered by mixed woodland and rough grassland, and caught only flying insects. In addition, however, thrips on vegetation, particularly Gramineae, were collected by hand sampling (Lewis, 1959*a*, 1960) and sweeping.

This paper is divided into two sections. In section I the species recorded at Silwood Park are listed together with the months (in roman numerals) during which they were caught flying. Biological details are given for some species. For many species further data on host plants and times of appearance on these can be obtained from Morison (1947–49). Most of the records were collected by the author; a few were collected by Mr. R. G. Davies and are denoted (*R.G.D.*). New records for Berkshire are marked with an asterisk. In section II the relationship between flight activity and type of habitat is discussed.

In 1956 and 1957, sixteen and five water traps, respectively, were exposed continuously from April to September. Two suction traps were run intermittently in 1956, 1957 and 1958. Most of the data in this paper are obtained from water trap catches. Some indication of the number of each species caught in all traps over the whole period is given by dividing the catches into five categories, thus: very large (V.L.) > 5000; large (L) 1000–5000; moderate (M) 100–1000; small (S) 5–100 and very small (V.S.) < 5. These categories cannot be used for a strict comparison of the relative abundance of different species flying over the traps, as some species were markedly attracted to white whilst other were not (Lewis, 1959), but they do give a reasonable indication of the numbers in which different species may be caught.

SECTION I

Suborder TEREBRANTIA

Family MELANTHRIPIDAE

**Melanthrips fuscus* (Sulzer). (M) ♀♀ v–ix, ♂♂ v–ix.

In 1956 maximum flight of females occurred v–vii, males v–vi. Only occasional specimens were taken at later dates. The sex ratio was approximately 1 : 1 in 1956 and 1957. The species may be attracted to white.

Family AEOLOTHRIPIDAE

Aeolothrips albicinctus Haliday. (V.S.) 1 ♀ (macropt.) vii.

More common on grasses in the apterous and micropterous forms.

**Ae. fasciatus* (L.). (M) ♀♀ v–ix, ♂♂ v–viii.

Ae. tenuicornis Bagnall. (M) ♀♀ v–viii, ♂♂ v–viii.

**Ae. gloriosus* Bagnall. *G. D. Morison* det. (V.S.) 1 ♀ vi, 1 ♀ ix.

A new record for Britain. The species was described by Bagnall (1914) from three females collected in Sardinia.

**Ae. melaleucus* Haliday. (V.S.) 1 ♀ v.

Family Thripidae

Chirothrips manicatus Haliday. (V.L.) ♀♀ v–ix, (S) ♂♂ vi–viii.

In 1956 there were two peaks of flight activity; the first when overwintered females emerged from hibernation in May and the second in July, probably as the females sought fresh host plants. Thirty-seven males, which are apterous, were caught in traps, suggesting that they too were dispersed by wind.

There was little flight after July (cf. *Limothrips cerealium* (Lewis, 1959*a*)), probably because the females seek hibernation sites on or near the grasses on which they develop. There was a preponderance of new generation males, which do not overwinter, on inflorescences of timothy in late July and August, 1957, where they remained until death. Their numbers decreased rapidly after the water content of the inflorescences dropped to approximately 49 per cent.

Both sexes were abundant on timothy (*Phleum pratense*) inflorescences, common on rye-grass (*Lolium perenne*) and cocksfoot (*Dactylis glomerata*) inflorescences, but occasional to rare on the foliage of these grasses and on wheat and oats. The appearance of females on cereals was largely confined to periods of great flight activity, when they were probably blown there. In 1957, ovarian dissections (Lewis, 1959*a*) showed that most overwintered females had died by mid-July. The number of females on rye-grass increased slightly towards the end of the season, as other grasses withered. Hibernating females were common on timothy stubble.

There was one generation per year. Morison (1943) recorded one generation in N.E. Scotland, but von Oettingen (1942) found two in N.E. Germany.

**C. hamatus* Trybom. (S) ♀♀ v–vi.

Both sexes occasional to common on meadow foxtail (*Alopecurus pratensis*). Females taken rarely on cocksfoot and wheat.

**Limothrips cerealium* Haliday. (V.L.) ♀♀ iv–ix, (S) ♂♂ vii–ix.

There are three periods of great flight activity associated with the movement of females from hibernation quarters in spring, their spread to fresh hosts in June and July, and the movement from these in August and September (Lewis, 1959*a*). A few males, which are apterous, were dispersed by wind.

Both sexes abundant on wheat and oats, occasional on rye-grass, timothy, cocksfoot and other grasses.

L. denticornis Haliday. (M) ♀♀ v–ix, (V.S.) ♂♂ vii.

In 1956 there were three marked periods of flight activity occurring simultaneously with those of *L. cerealium*. They probably correspond to similar stages in the annual cycle of this species.

Common on wheat, occasional on timothy and rye-grass.

**Dendrothrips ornatus* (Jablonowski). (V.S.) ♀♀ vii–viii.

Aptinothrips rufus (Gmelin). (V.S.) ♀♀ vii–viii.

Both sexes are apterous. There was little dispersal by wind. It was occasional to common on timothy, rye-grass, cocksfoot, wheat and oats. Three males were taken on timothy in June and July and one on rye-grass in July.

A. stylifer Trybom.

Rare. 1 ♀ and 1 ♂ on meadow foxtail, in May. (*R.G.D.* coll. and det.)

**A. obscurus* (Müller). (M) ♀♀ v–ix.

Maximum flight activity and peak numbers on grasses occurred in July. Common on cocksfoot, occasional on rye-grass, timothy, wheat and oats. Four brachypterous specimens were taken on grass from July to September, 1957.

**Odontothrips cytisi* Morison. ♀♀ on *Sarothamnus scoparius* vi.

O. ulicis (Haliday). ♀♀ on *Ulex* sp. vi.

O. meridionalis Priesner. 1 ♂ June (*R.G.D.* coll. and det.).

Taeniothrips sp. Very large numbers of *Taeniothrips* sp. were caught in the water traps in 1956 and 1957, and large numbers in suction traps in 1957 and 1958. The two most common species, which were strongly attracted to white, were *Taen. atratus* and *Taen. vulgatissimus*, and their numbers were so large that estimates of the relative proportion of these two species have been based on the identification of sub-samples. Thus, first appearance dates, peaks of flight activity and perhaps the presence of less common species in the genus may have been overlooked.

Taen. atratus (Haliday). (V.L.) ♀♀ v–viii, (V.L.) ♂♂ v–vi.

Taen. vulgatissimus (Haliday). (V.L.) ♀♀ vi–viii, (V.L.) ♂♂ vi.

Taen. (*Rhopalandrothrips*) *consociatus* (Targioni-Tozzetti). (V.S.) 1 ♂ vi.

Thrips sp. The number of specimens caught in 1956 was so large that identification was impractical. The number given for each species is merely an estimate based on the identification of sub-samples. Less common species and sexes may have been overlooked. Numbers were not counted in 1957. Some species, probably all those listed below, are attracted to white (Lewis, 1959). No attempt has been made to give the peaks of flight activity or sex ratios for different species, and flight periods almost certainly extend over more months than indicated.

Thrips hukkineni Priesner. (L) ♀♀ v–vi.

T. physapus L. (None identified from traps.) 4 ♀♀ on *Taraxacum officinale*, iv. (*R.G.D.* coll. and det.)

**T. praetermissus* Priesner. (L) ♀♀ v–vi.

T. fuscipennis Haliday. (L) ♀♀ v.

T. major Uzel. (V.L.) ♀♀ vi–vii, (V.L.) ♂♂ vi–vii.

**T. tabaci* Lindeman. (L) ♀♀ v, (L) ♂♂ v.

Stenothrips graminum Uzel. (L) ♀♀ v–vii, (M) ♂♂ v–vii.

There were no distinct peaks of flight activity during the flight period, which for males was about three weeks shorter than for females.

Both sexes overwinter as larvae (Kurdjumov, 1913) or possibly adults (Kolobova, 1926) in the soil. They emerge from hibernation as adults in spring. No females were found on oats, the host plant, before flight had been recorded, but the rapidity with which females reached laying condition after flight was first noticed (within 16 days 91 per cent. of females on oats were laying) suggests that thrips fed and possibly mated before flight.

The sex ratios of catches in water traps, suction traps, and on oats were markedly different (Table I).

TABLE I.—*Numbers of* S. graminum *caught and the sex ratio in water traps, suction traps and on oats*

	Year	Total catch	Approximate ratio ♀ : ♂
Water trap . .	1956	670	6 : 1
	1957	183	4 : 1
Suction trap . .	1957	191	47 : 1
	1958	777	36 : 1
Oats . . .	1957	304	19 : 1

Relatively more males were caught in white water traps than in suction traps, which indicates that males may be more attracted to white than females. (This was not apparent in a previous analysis of data from different coloured traps (Lewis, 1959) as most of the few *S. graminum* caught then were females. They were not markedly attracted to white).

On 24.vi.57, 15 out of 60 females from oats were infested by a nematode (family : Allantomatidae, *det.* D. Clements). The sac-shaped females, males and many larval forms were present in the insects' abdomen. This is a new record for *S. graminum* in Britain, though in Russia Kolobova (1926) found specimens of *S. graminum* infested by an unidentified nematode " acquired " in the soil. She found infested specimens were unable to reproduce.

Frankliniella intonsa (Trybom). (L) ♀♀ iv–ix, (S) ♂♂ vi–ix.

There was one marked peak of flight activity from early to mid-May, 1956. The sex ratio in white water traps in 1956 was approximately 37 ♀ : 1 ♂. The species is probably attracted to white.

**F. tenuicornis* (Uzel). (S) ♀♀ vi–ix, (S) ♂♂ vi–ix.

The sex ratio of suction trap catches in 1957 was approximately 6 ♀ : 1 ♂, and of white water trap catches 10 ♀ : 1 ♂.

**Kakothrips robustus* (Uzel). 1 ♂ on cultivated peas, vi. (*R.G.D.* coll. and det.)

Suborder TUBULIFERA

Family PHLAEOTHRIPIDAE

Phlaeothrips ulmi (Fabr.). (S) ♀♀ vi–ix, (V.S.) 1 ♂ vii.

Ph. fungi (Degeer). (V.S.) 1 ♀ vii, 1 ♂ vii. One micropterous female under bark, iv. (*R.G.D.* coll., *G. D. Morison* det.)

Haplothrips subtilissimus (Haliday). (S) ♀♀ v–ix.

**H. distinguendus* (Uzel). (V.S.) 1 ♀ vii, 1 ♂ vii, 2 ♂♂ iv on " vegetation ". (*R.G.D.* coll., *G. D. Morison* det.)

**H. setiger* Priesner. (S) ♀♀ v–vi, (V.S.) v–vii.

**Euphlaeothrips coriaceus* (Haliday). (V.S.) 1 ♀ v. (*G. D. Morison* det.)

**Hoplandrothrips annulipes* (Reuter). (V.S.) 1 ♂ vi. (*G. D. Morison* det.)

**H. bidens* (Bagnall). Both sexes under old bark of *Sarothamnus scoparius*.

Megathrips lativentris (Heeger). 1 ♀ on *Ulex europaeus* iv. (*R. Dobson* coll., *R.G.D.* det.)

SECTION II

In Table II the numbers of thrips trapped, the habitat type and abundance group are given for 33 species recorded at Silwood Park. The habitats frequented by the species listed can be divided into two broad types :

(1) Permanent (*P*), *i.e.* trees and woody shrubs : these include habitats of the species feeding on fungi and living on or under bark, and predatory species confined to trees.

(2) Temporary (*T*), *i.e.* annuals and flowers, including grass inflorescences. A species can be described as either abundant (*A*), common (*C*), occasional (*O*) or rare (*R*) according to the frequency with which it generally occurs on its hosts. The terms denoting abundance are mainly those used by Morison (1947–49), except that his designation " numerous " is equivalent to " occasional " in this section, and for *Dendrothrips ornatus* those of Fowler (1954), modified in the light of local experience. Species in which brachypterous, micropterous and apterous forms predominate in

both sexes, and predatory species not confined to a particular type of habitat, have been excluded together with *Limothrips cerealium*, which was abundant on the wheat surrounding the traps. Species recorded on vegetation but not caught in flight are included.

White traps catch about 100 times more *Taen. vulgatissimus* and *Taen. atratus* than black traps, and about 30 times more *Thrips* sp. (Lewis, 1959). Assuming that all *Taeniothrips* sp. and *Thrips* sp. are attracted to a similar extent, catches of these two genera (except *Taen. consociatus*) were divided by 100 and 30 respectively to give a more correct, though still very approximate, estimate of the relative numbers flying over the traps (Table II). *Melanthrips fuscus*, *Stenothrips graminum* (males) and *Frankliniella intonsa* are also probably attracted to white, but to what extent is unknown and catches were not corrected. In any case their total numbers are small compared with *Taeniothrips* sp. and *Thrips* sp.

TABLE II.—*Total and corrected catches from white water traps, with habitat types and abundance groups for each species*

	Total catch	Habitat type	Abundance group on hosts	Approximate corrected catch
Melanthrips fuscus	393	*T*	*O*	393
Chirothrips manicatus	3,560	*T*	*A*	3,560
C. hamatus	23	*T*	*O*	23
Limothrips denticornis	399	*T*	*C*	399
Dendrothrips ornatus	1	*P*	*C*	1
Anaphothrips obscurus	196	*T*	*C*	196
Odonothrips cytisi	.	*P*	*C*	.
O. ulicis	.	*P*	*C*	.
O. meridionalis	.	*P*	*C*	.
Taeniothrips atratus	11,998	*T*	*A*	120
Taen. vulgatissimus	14,687	*T*	*A*	147
Taen. consociatus	1	*P*	*C*	1
Thrips physapus	.	*T*	*C*	.
T. hukkineni	2,700	*T*	*C*	90
T. praetermissus	4,500	*T*	*O*	150
T. fuscipennis	3,500	*T*	*C*	117
T. major	22,000	*T*	*C*	733
T. tabaci	2,700	*T*	*C*	90
T. flavus	480	*T*	*C*	16
Stenothrips graminum	853	*T*	*C*	853
Franklinella intonsa	3,423	*T*	*C*	3,423
F. tenuicornis	145	*T*	*O*	145
Kakothrips robustus	.	*T*	*O*	.
Phlaeothrips ulmi	60	*P*	*O*	60
Ph. fungi	2	*P*	*O*	2
Ph. corticis	.	*P*	*O*	.
Haplothrips subtilissimus	10	*P*	*O*	10
H. distinguendus	2	*T*	*R*	2
H. setiger	15	*T*	*O*	15
Euphlaeothrips coriaceus	1	*P*	*R*	1
Hoplandrothrips annulipes	1	*P*	*C*	1
H. bidens	.	*P*	*O*	.
Megathrips lativentris	.	*P*	*R*	.

Species in the abundant and common groups were separated into those from permanent and temporary habitats, and the corrected catches divided by the number of species in each habitat type. This was repeated for the occasional group (Table III).

Table III.—*The relationship between mean catch per species and habitat type for thrips from different abundance groups*

Abundance group	Habitat type	Number species	Corrected total catch	Mean catch per species
Abundant and common .	*P*	6	3	0·5
	T	13	9,744	750
Occasional . . .	*P*	5	72	14·4
	T	6	726	121

The mean catch per species is clearly much higher for species from temporary habitats than for those from permanent ones. Allowing for the assumptions and approximations mentioned above, this indicates that migration is generally most common in species of thrips associated with temporary habitats. Some species may live and require food over many months, so, if they feed on hosts favourable for only a few days or weeks, migration is essential. On trees and woody plants a food supply is likely to be available for a long period, precluding the need for such frequent dispersal. This agrees with data collected for other groups of terrestrial arthropods by Southwood (*in press*) which suggests that migration is an evolutionary necessity for denizens of temporary habitats.

Of the temporary habitats mentioned, grass inflorescences, on the whole, remain favourable for longer periods than flowers. This persistence is perhaps reflected in the behaviour of the grass-dwelling species studied (e.g. *L. cerealium*, *L. denticornis*, *C. manicatus* and *S. graminum*) whose dispersal is confined to one, two or three relatively short periods in the life cycle. On the other hand, many flower-dwelling species appear willing to fly more generally throughout late spring and summer. In Australia this was shown to be particularly true for the flower-dwelling *Thrips imaginis* Bagnall, which often flew from suitable hosts—fresh, uncrowded flowers—without any apparent stimulus other than an urge to disperse (Davidson and Andrewartha, 1948).

Acknowledgments

Thanks are due to Prof. O. W. Richards, F.R.S., for facilities provided at Imperial College Field Station and to Dr. T. R. E. Southwood for suggesting the treatment of the data given in section II. Dr. Guy D. Morison of Marischal College, Aberdeen, kindly identified some specimens and Mr. R. G. Davies provided additional records.

References

Bagnall, R. S., 1914, Brief descriptions of new Thysanoptera—IV. *Ann. Mag. nat. Hist.* (8) **14** : 375–81.

Davidson, J. and Andrewartha, H. G., 1948, The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). *J. Anim. Ecol.* **17** : 200–22.

Fowler, V. W., 1954, Notes on some pests observed in the course of advisory work at Wisley during 1953. *J.R. hort. Soc.* **79** : 405–8.

Kolobova, A. N., 1926, *Stenothrips graminum* Uzel. *Trans. Poltava Agric. Expt. Sta.* **49** : 26 pp. (cf. *Rev. appl. Ent.* (*A*) **14** : 606–7.)

Kurdjumov, N. V., 1913, The more important insects injurious to grain crops in Middle and South Russia. *Studies from Polatava Expt. Stn.* **17** : 119 pp. (cf. *Rev. appl. Ent.* (*A*) **2** : 170–3.

Lewis, T., 1959, A comparison of water traps, cylindrical sticky traps and suction traps for sampling thysanopteran populations at different levels. *Ent. exp. appl.* **2** : 204–15.

LEWIS, T., 1959*a*, The annual cycle of *Limothrips cerealium* Haliday (Thysanoptera), and its distribution in a wheat field. *Ibid :* **2** : 187–203.

—— 1960, A method for collecting Thysanoptera from Gramineae. *Entomologist* **93** : 27–8.

MORISON, G. D., 1943, Notes on Thysanoptera found on flax (*Linum usitatissimum* L.) in the British Isles. *Ann. appl. Biol.* **30** : 251–9.

—— 1947–49, Thysanoptera of the London Area. *Lond. Nat.* (suppl.) **1947** : 1–36 ; *Ibid.* **1948** : 37–75 ; *Ibid.* **1949** : 77–131.

OETTINGEN, H. VON, 1942, Die Thysanopteren des norddeutschen graslands. *Ent. Beih Berl. Dahlem.* **9** : 79–141.

SMITH, K. G. V., 1957, A preliminary list of the Thysanoptera of Oxfordshire and Berkshire. *Proc. Ashmol. nat. Hist. Soc.* **1951–56** : 19–26.

SOUTHWOOD, T. R. E. (*in press*), Migration—an evolutionary necessity for denizens of temporary habitats. *Proc. XIth Int. Congr. Ent.*

TAYLOR, L. R., 1951, An improved suction trap for insects. *Ann. appl. Biol.* **38** : 582–591.

OBSERVATIONS ON THE BIOLOGY OF *PERILITUS DUBIUS* (WESMAEL) (HYMENOPTERA : BRACONIDAE), A PARASITE OF THE CHRYSOMELID BEETLE *PHYTODECTA OLIVACEA* (FORSTER)

By N. Waloff
(*Imperial College, London*)

Perilitus dubius (Wesmael) is a parasite in its larval stages of the Chrysomelid beetle *Phytodecta olivacea* (Forster). In the five years of the study of the host, only five wasps have been seen in the field on the beating trays (Richards, 1960). This must be due to the elusive behaviour of the adult parasite, as its larvae occurred in many beetles, and in the laboratory the wasps were bred out of the hosts collected in four successive years. The most extensive accounts relating to the genus *Perilitus* (=*Dinocampus*) are those of *D. rutilus* Nees (Jackson, 1928, 1935) and of *D. coccinellae* Schrank (Ogloblin, 1913, 1924 ; Balduf, 1926) and most of the available data on the genus are summarised by Clausen (1940).

The adult of *P. dubius* (Wesmael) has recently been re-described by Richards (*loc. cit.*) and a short description of the larva is given in this paper.

Method of Rearing the Parasite

There are two generations in the year of the adult host beetles, which live on broom, *Sarothamnus scoparius* (L.) Wimm. The beetles were collected at Silwood Park, Sunninghill, Berkshire and the weekly collections were divided into two ; some were preserved in alcohol for later dissections and the rest were kept alive in large jars with cuttings of broom. The floors of the jars were lined with a mixture of sand and bulb fibre which was watered at intervals, and in which the beetles over-wintered. The jars were kept at out-of-doors temperatures throughout the winter and returned to the laboratory in April.

The Larva

The preserved specimens of the white, caudate first instar larvae are 0·8 mm. long and 0·09 mm. broad ; the yellowish, fully-grown larvae reach the length of 4·5–5·0 mm. and are 1·5 mm. broad. Figure 1 depicts a flattened head of a fully grown larva. I am most grateful to Dr. J. R. T. Short for examining the larvae of *P. dubius* (Wesmael), which I sent to him. He agrees that, in contrast to the larvae of the few species of *Perilitus* which have been described so far (Short, 1952 ; Grandi, 1931 ; Goidanich, 1933), *P. dubius* has a head capsule with only a moderately sclerotised hypostoma and an unsclerotised stipital sclerite.

The Number of Annual Generations of *P. dubius*

On no occasion did the adult parasite emerge in the same year as the hosts were collected. In the laboratory there were two main periods of emergence, the first in May of the following year and the second a month or more later. The May wasps emerge out of the spring generation of beetles, the June ones out of the autumn generation and out of some of the late members of the spring generation (Table I). It thus seems that the length of development and the time of emergence of *Perilitus* is in some way controlled by the host beetles, as for instance is that of *Diplazon* by its Syrphid hosts (Schneider, 1951). It is thought that the dates of the emergences in the laboratory are well in advance of those in the field, as the parasitised beetles were collected between the following dates :—21.vi–11.x.54, 24.vi–13.x.55, 5.vi.–16.x.56, 12.vi.–10.ix.57 and 17.vi.–9.ix.58. Eggs of the Braconid within the hosts were found on 12.vi.58, 8.vii.57, 22.vii.55, 13.viii.57, 18–25.viii.55, 26.viii.58, 2.ix.58, 18.ix.56, 20.ix.54, 22–23.ix.55 and 2.x.56, while five adult wasps were collected in the field on 15.v.58 (1♂), 5.vii.56 (1♀), 5.viii.58 (1♀), 19.viii.58 (1♀) and on 4.ix.56 (1♀). The difference between the laboratory and the field dates cannot be explained by the longevity of the wasps, as, at least in captivity, most of them lived for under a fortnigh.

Table I.—*Dates of emergence of* Perilitus dubius *in the laboratory, from the adults of* Phytodecta olivacea *collected in the previous year*

Dates of collection of *Phytodecta*	Dates of emergence of *Perilitus*	Dates of collection of *Phytodecta*	Dates of emergence of *Perilitus*
24.vi–22.vii.55	7–9.v.56	29.vii–11.viii.55	18.vi–2.vii.56
5.vi–24.vii.56	8–22.v.57	7.viii–25.ix.56	17.vi–25.vi.57
6.vi–2.vii.57	12–16.v.58	—	—
17.vi–1.vii.58	6–7.v.59	23.vii.58*	4–5.vi.59
—	—	5.viii–9.ix.58	10–29.vi.59

* Spring generation of beetles.

It is of interest that *P. dubius* will oviposit in the larvae of the host as well as in the adults and we have bred two adult wasps from the larvae of *Phytodecta* collected on 6.viii.57, the adult parasites (1♂, 1♀) emerging in the following year, 26.vi.58.

Thus the available evidence indicates that there is only one annual generation of *P. dubius*, although its emergence is spread out over a considerable period of time. In contrast to this species, *Dinocampus* (=*Perilitus*) *coccinellae* Schrank is considered by Ogloblin (1913) and Balduf (1926) to go through four to five generations a year, while Jackson (1928) found that there are two to three annual generations of *Perilitus* (=*Dinocampus*) *rutilus* Nees. She states that in the summer the whole developmental period lasts only a month, while in autumn and winter it can be as long as eight months. Adults of *Phytodecta* dissected in August, September, February and March contained fully grown larvae of *P. dubius* hibernating inside the diapausing hosts.

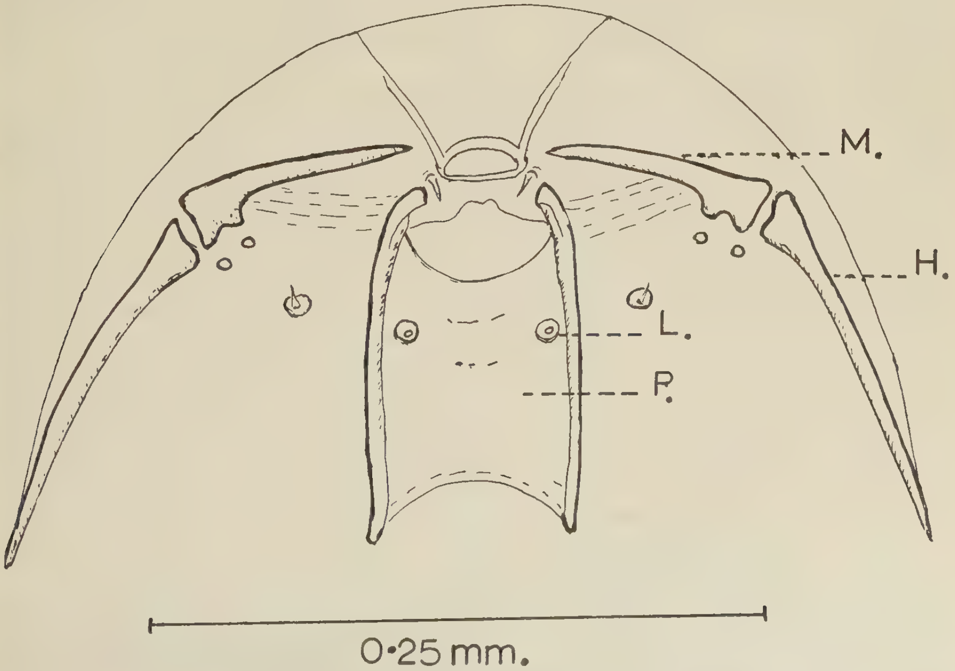


Fig. 1.—Flattened head capsule of *Perilitus dubius* (Wesmael). *M*, mandible; *H*, hypostoma; *L*, labial palp; *P*, prelabium.

SEX RATIO OF THE WASPS

Altogether 136 adult wasps emerged in four years, the numbers in each year being :—17♂ 19♀, 1956 ; 15♂ 25♀, 1957 ; 5♂ 12♀, 1958 ; 17♂ 26♀, 1959. Each year there was a slight preponderance of the females and the average sex ratio was 1 male : 1·52 females. It still remains unknown whether, in common with the other species of the genus, *P. dubius* can reproduce parthenogenetically.

METHODS OF KEEPING THE ADULTS AND LONGEVITY OF THE CAPTIVE WASPS

After emergence, the wasps were placed in three by one inch tubes, or in seven-pound jars covered with muslin. In either case there was slightly moistened sand on the floor of the containers, which also held twigs of broom (in flower in May) and a small piece of raisin pinned to the muslin. A tube filled with cotton wool soaked in dilute honey water and covered with muslin was introduced into the jars, whereas small strips of filter paper moistened with dilute honey were placed for an hour a day in the tubes. There was no difference in the longevity of *Perilitus* in the tubes and in the jars and most of them lived for a short time only (*see* Table II). Two of the longest lived males survived for 10 days and the females up to 17. Ogloblin (1913) reports that some *P. coccinellae* lived up to 20 days whereas most of those reared by Balduf (1926) survived for four to five. Jackson (1928) says that the adults of *P. rutilus* lived for about a fortnight, but a few survived for three to four weeks.

TABLE II.—*Longevity of* Perilitus dubius (♂♀) *in captivity*

Longevity (days) .	5	6	7	8	9	10	12	13	17
No. of *P. dubius* .	4	13	23	6	13	5	1	4	1

BEHAVIOUR OF ADULT *Perilitus* AND OVIPOSITION

Perilitus will readily drink moisture on cut raisins and dilute honey water on filter paper, or on cotton wool. The wasps copulate a few hours after emergence and the females are ready to oviposit on the day of emergence. A number of observations (52 occasions, 22♀) were made and their preoviposition and oviposition behaviour is described below.

When a mated *Perilitus* female is introduced into a horizontal tube with *Phytodecta* it immediately becomes agitated. It raises itself slightly on its legs, begins to vibrate its antennae and cleans its ovipositor. It may jump and give a short flight, after which it follows every movement of the host, occasionally palpating the beetle's abdomen with its antennae. Alternately, if the beetle is feeding, it may settle near to it, palpate its abdomen and, if the beetle moves away, follow it closely. In pursuit of the host the ovipositor may be unsheathed and brought forward to project under the head, or this action may be delayed until the wasp encounters the beetle " face to face ". In either case, after the period of pursuit the wasp springs forward and, on facing the host, palpates its head violently. The beetle then vibrates its antennae extremely rapidly and either drives off the wasp or extends its head, exposing the membrane between it and the thorax, into which the Braconid thrusts its ovipositor. The eggs are then laid in the thorax of the host. In oviposition, the wasp utilises part of the inherent pre-mating behaviour of *Phytodecta olivacea*, as before copulation the beetles face one another and palpate one another with their antennae.

In 45 out of the 52 recorded instances of oviposition, the ovipositor was inserted between the head and thorax, in 4 in the pleural membrane between the thorax and the abdomen, in 3 in the abdomen, close to the anus. Thus there is variation in the oviposition behaviour of *P. dubius* and the species appears to have evolved a mechanism which is not usual in the other members of the genus which have been studied so far (*see* Clausen 1940 : 28).

Oviposition may consist of a single insertion of the ovipositor or up to four swift thrusts. The process is short and may last a fraction of a second. In 26 instances it lasted between one and eight seconds and in 5 others between ten and sixty. Two of the wasps remained attached to the moving beetles for two and for two and a half minutes respectively. After each oviposition the wasps clean their ovipositors and in this process some of the host fluids are probably transferred to the parasite.

It was noted that not only the females but also the males of *P. dubius* would pursue the moving beetles and palpate them with their antennae. The female wasps were stimulated by any moving objects of a small size and would pursue a small piece of cork dragged along on a fine wire. When the piece of cork was smeared with the contents of a *Phytodecta, Perilitus* flew and alighted on it, but later " disregarded " it. It was noted that in the pursuit of the cork the wasp did not bring forward its ovipositor. Bryden and Bishop (1945), who made the first observations on the oviposition of *P. coccinellae* in Great Britain, considered that movement is the principal stimulus to parasitisation, but probably it only provides the initial stimulus and both the chemical and the tactile senses are more important in the later stages of the oviposition behaviour.

On one occasion, four *Perilitus* females were placed in tubes with *Sitona regensteinensis* Hbst., four others in tubes with a *Sitona* and a *Phytodecta* in each, and one other with *Coccinella septempunctata* L. In tubes with *Sitona* alone and with the ladybird, *Perilitus* pursued the moving beetles but did not oviposit in them. In tubes with *Sitona* and *Phytodecta* the wasp followed the movements of either beetle, but in three tubes it oviposited in *Phytodecta* only. In the fourth tube *P. dubius* attempted to oviposit in *Sitona*. It is probable that the movements of the beetle, accompanied by the " smell " of *Phytodecta* in the confined space of the tube, provided a sufficient stimulus to elicit this behaviour.

It was also repeatedly seen that *Perilitus* would lay in already parasitised beetles, even when they were given the option of unparasitised ones. There is also some evidence from the dissections of the field beetles that oviposition can occur in parasitised hosts, as in three beetles the eggs of *Perilitus* were found together with fully grown larvae. Twelve other probable, but not certain, instances of this were encountered in 323 parasitised hosts.

THE NUMBER OF OVIPOSITIONS EFFECTED BY A SINGLE WASP

Observations were made on two *Perilitus* females for three continuous days. The host beetles offered to them were reared in the laboratory and hence not previously parasitised. The first *Perilitus* oviposited in 9 beetles on the first day, in 2 on the second and in 3 on the third ; it was then left with one other beetle for two days. The second *Perilitus* oviposited in 8 beetles on the first day, in 7 on the second and in 4 on the third. It was also left with a beetle for the fourth and fifth days. The two beetles presented to the wasps on the fourth and fifth days were dissected three months later ; the first contained 9 and the second 10 parasitic larvae. These numbers correspond with a minimum of three ovipositions by each wasp. Thus the first female oviposited at least 17 times, and the second one 22. The number of Braconid larvae resulting from the ovipositions of the first wasp was 51, and that from the second one 58. The rate of oviposition on successive days was falling off with the age of the parasite and Balduf (1926) also came to the conclusion that the responsiveness of the parasite waned as it grew older.

THE NUMBER OF *Perilitus* EGGS AND LARVAE PER BEETLE

The number of eggs laid in one host by the members of the genus *Perilitus* can be very large and Ogloblin (1924) found up to 70 eggs of *P. coccinellae* in one ladybird. As has been described by Ogloblin (1924) and by Jackson (1928), the minute eggs enlarge up to one thousand times by volume in *P. coccinellae* and twelve hundred times in *P. rutilus*. The number of larvae per host differs greatly in the different species of this genus. Giard (1895) says that about 50 larvae of *P. sicheli* Giard were found in *Timarcha tenebricosa* (Fab.), Grandi (1931) found up to 11 larvae of *P. morimi* Ferr. in the Cerambycid *Morimus asper* Sulz, and Goidanich (1933) up to 20 larvae in the same host. Only one larva of *P. rutilus* (Jackson, 1928) normally develops in *Sitona lineatus* L.

The number of eggs laid by *P. dubius* has been deduced from the numbers found in the thorax of the host beetles. If the minute, newly-hatched larvae in the thorax are also considered, further evidence is obtained of this number. The larvae which were included in these counts were no bigger than those in the enlarged egg membranes and had not yet made their way from the thorax to the abdomen (*see* Table III).

TABLE III.—*Eggs and recently hatched larvae in the thorax of* Phytodecta, *serving as indices of the number of eggs laid by* Perilitus dubius, *Silwood Park, Sunninghill, Berkshire,* 1954–58

No. *Perilitus* eggs and minute larvae in thorax of host	1	2	3	4	5	7
No. hosts	17	22	19	6	3	1

From the data collected it may be assumed that one to three eggs are laid simultaneously, although five have also been encountered. One field beetle contained as many as seven minute larvae and eggs, but it is not known whether they resulted from one or from two ovipositions.

The commonest number of larvae per host was two or three (*see* Table IV) and this was further confirmed by dissections of the overwintering beetles parasitised in the laboratory in 1959. Balduf (1926) has repeatedly observed destruction of supernumerary larvae of *P. coccinellae* but, as in the course of the dissections given in Table IV, 383 small and 363 fairly large or large larvae were encountered, it seems that the destruction of supernumeraries is less frequent in *P. dubius*. However, there was a tendency for more larvae to develop in the female beetles than in the smaller *Phytodecta* males. In the 311 parasitised beetles encountered in 1954–58, the average number of parasitic larvae per male was 2·4, and that per female 2·7.

TABLE IV.—*Number of* Perilitus dubius *larvae per host beetle.* Dissections 1954–59

No. of *Perilitus* larvae per host	1	2	3	4	5	6	7
No. of occurrences in spring generation beetles	16	43	68	12	3	0	0
No. of occurrences in autumn generation beetles	26	63	70	14	5	2	1
Total occurrences	42	106	138	26	8	2	1

Only five records are available of the numbers of wasps hatching from isolated hosts, as most of the beetles were kept in groups. Four isolated hosts produced one wasp each and one beetle produced two.

EFFECTS OF PARASITISM ON THE HOST BEETLE

The small larvae which originally lie in the thorax of the beetle move down into the abdominal haemocoele, where they complete their development. Pupation is in the soil and the adult *Perilitus* emerges in the following year. As has been described by Jackson (1928, 1935) and by Ogloblin (1924), the embryonic membrane still encloses the larva after hatching, but dissociation takes place and the cells maintain an independent existence. They enlarge, proliferate and form the food of the larvae. The ovaries of the parasitised beetles become reduced, the internal organs of the host exhausted, the thoracic muscles appear as thin threads and eventually the beetles are killed by the parasite. Larger coccinellid beetles do not usually die for some time after the emergence of *P. coccinellae*, although they rarely show ovaries in functional condition (Balduf, 1926). Timberlake (1916) records an interesting case in which two generations of *Dinocampus* (= *Perilitus*) *americanus* (Riley) were reared from the same ladybird.

PERCENTAGE PARASITISM OF THE HOST POPULATION

The life history of the host of *P. dubius*, *i.e.* of *Phytodecta olivacea* Forst., has already been described (*see* Waloff and Richards, 1958) and it is only briefly recapitulated here. In the spring the beetles emerge from hibernation in the soil and live and reproduce on broom. The survivors of the spring adults hibernate for a second time. The new adults, or the autumn generation of beetles do not reproduce in the same year, but feed and hibernate in the soil. A population of *Phytodecta* was studied at Silwood Park, Sunninghill, Berkshire and the percentage of parasitisation by *P. dubius* was determined by dissecting beetles collected weekly throughout the season (*see* Table V). With the exception of 1958, the spring generation of the beetles was more lightly parasitised than the autumn one, but this aspect of parasitism is discussed in a paper on the natural population of *P. olivacea* (Richards and Waloff, 1961).

TABLE V.—*Number of* Phytodecta olivacea *dissected* (*in brackets*) *and percentage parasitism by* Perilitus dubius

Year	Spring generation		Autumn generation	
1954	(409)	5·6	(375)	11·5
1955	(522)	5·5	(404)	9·9
1956	(565)	4·8	(119)	26·4
1957	(304)	13·1	(194)	17·6
1958	(510)	6·5	(112)	5·0

SUMMARY

Perilitus dubius (Wesmael) is a parasite in its larval stages in the adult of the Chrysomelid beetle *Phytodecta olivacea* (Forster). Two wasps (1♂, 1♀) have also been reared from the larvae of the host.

As far as has been determined there is only one annual generation of the Braconid, but its emergence is protracted and it attacks the adults of both the spring and the autumn generations of the host.

One hundred and thirty-six wasps were reared in the laboratory; these mostly lived for less than a fortnight, but one female survived for 17 days. The sex ratio was 1 male : 1·52 females.

Oviposition is effected by the insertion of the ovipositor in the pleural membrane between the head and the thorax of the host. The eggs and the newly hatched larvae are found in the thorax of the beetle, the older larvae in the abdominal haemocoele. They hibernate inside the beetle and emerge in the following year. The most usual number of larvae per host is two or three, although between one and seven have also been found. The head capsule of a fully grown larva is figured.

REFERENCES

BALDUF, W., 1926, Bionomics of *Dinocampus coccinellae* Schrank. *Ann. ent. Soc. Amer.* **19** : 465–98.

BRYDEN, J. W. and BISHOP, M. W. H., 1945, *Perilitus coccinellae* (Schrank) (Hym., Braconidae) in Cambridgeshire. *Ent. mon. Mag.* **81** : 51–52.

CLAUSEN, C. P., 1940, *Entomophagous insects.* New York.

Giard, A., 1895, Sur quelques espèces nouvelles d'Hyménoptères parasites. *Ann. Soc. ent. France* **64** : lxxvi–vii.

Goidanich, A., 1933, Materiali per lo studio degli Imenotten Braconidi I. *Boll. Laboratorio di Entomologia* **6** : 33–50.

Grandi, G., 1931, Scoperta di un nuovo Braconidae (*Perilitus morimi* Ferr.) parassita degli adulti del *Morimus asper* Sulz. (Coleoptera–Cerambycidae) e descrizione della sua Larva. *Ibid.* **4** : 1–4.

Jackson, D. J. 1928, The biology of *Dinocampus* (*Perilitus*) *rutilus* Nees, a Braconid parasite of *Sitona lineata* L. I. *Proc. zool. Soc.* **1928** : 597–630.

—— 1935, Giant cells in insects parasitised by Hymenopterous larvae. *Nature, Lond.* **135** : 1040–41.

Ogloblin, A. A., 1913, Contribution to the biology of the Coccinellidae. *Russ. ent. Obozr.* (*Rev. russe d'Ent.*) **13** : 27–43 [*in Russian*].

—— 1924, Le rôle du blastoderme extra-embryonnaire du *Dinocampus terminatus* Nees pendant l'état larvaire. *Mém. Soc. Sci. Bohème* **1924** : 1–27.

Richards, O. W., 1960, On some British species of *Perilitus* Nees (Hymenoptera : Braconidae). *Proc. R. ent. Soc. Lond.* (B) **29** : 140–4.

—— and Waloff, N., 1961, A study of a natural population of *Phytodecta olivacea* (Forster) (Coleoptera, Chrysomeloidea). *Phil. Trans.* (B) **244** : 205–57.

Schneider, F., 1951, Einige physiologische Beziehungen zwischen Syrphidenlarven und ihren Parasiten. *Z. angew. Ent.* **33** : 150–62, 6 figs.

Timberlake, P. H., 1916, Note on an interesting case of two generations of parasite reared from the same individual host. *Canad. Ent.* **48** : 89–91.

Short, J. R. T., 1952, The morphology of the head of larval Hymenoptera with special reference to the head of Ichneumonoidea, including a classification of the final instar larvae of the Braconidae. *Trans. R. ent. Soc. Lond.* **103** : 27–84, 34 figs.

Waloff, N. and Richards, O. W., 1958, The biology of the Chrysomelid beetle, *Phytodecta olivacea* (Forster) (Coleoptera : Chrysomelidae). *Trans. R. ent. Soc. Lond.* **110** : 99–116.

THE BIOLOGY OF THE BRITISH SPECIES OF THE GENUS OLYNX FÖRSTER (HYMENOPTERA: EULOPHIDAE), WITH A NOTE ON SEASONAL COLOUR FORMS IN THE CHALCIDOIDEA

By R. R. Askew

(*Hope Department of Entomology, University Museum, Oxford*)*

In a taxonomic revision of the genus *Olynx* (Askew, 1959) six species known from Britain, *O. arsames* (Walk.), *O. skianeuros* (Ratz.), *O. trilineata* Mayr, *O. euedoreschus* (Walk.), *O. gallarum* (L.) and *O. pulchra* Mayr., were redescribed. As a result of biological investigations it has since been discovered that one of these, *O. pulchra*, is an alternate generation of *O. gallarum*. *O. gallarum* was described in 1761, *O. pulchra* in 1877, and therefore *O. gallarum* must take priority. *O. pulchra* is referred to in this work as *O. gallarum* f. *pulchra* Mayr.

So far as is known, all the insects in the genus *Olynx* are parasitic in Cynipid galls on *Quercus*, where they feed, externally only, on the gall-making larvae. Giraud (Laboulbène, 1877) bred, from galls of *Bathyaspis aceris* Förster on *Acer*, a Eulophid which he named *Olynx acerinus*. He did not describe this species, which is almost certainly *Aulogymnus aceris* Förster, bred by Mayr (1877) from galls of the same Cynipid. The genera *Olynx* and *Aulogymnus* are closely allied.

All the field observations in this study were made in Wytham Wood, Berkshire in 1958 and 1959, in an area known as " Interplant " which contained several mature oak trees (*Quercus robur* L.), rather widely dispersed over a slope with a slight northerly inclination densely clothed in bramble, bracken, honeysuckle and sallow. The oak trees, because of the space afforded to each, were large-crowned, with their lower branches terminating in many cases only a few feet above the ground.

The Immature Stages

Eggs of *O. arsames* and *O. euedoreschus* have been examined. These are white, with unpigmented and unsculptured chorions. The egg of *O. arsames* (fig. 7) is bluntly pointed at either end with a slight concavity on one side, and 0·30 mm. long. The egg of *O. euedoreschus* (fig. 4) differs only in being rather larger (0·35 mm. long) and in having a small, nipple-like projection at the broader end.

The first instar larvae of *O. arsames* and *O. euedoreschus* (fig. 6) are flattened dorso-ventrally with thirteen segments after the head. The terminal segment is bilobed, the mandibles are small and simple, and the body is hairless without protuberances of any sort. All first stage Eulophid larvae described by Parker (1924)—*Melittobia acasta* Walk., *Tetrastichus* sp., *T. xanthomelaenae* Rond., *Oxymorpha intermedia* Thoms., *Tetrastichus ovivorax* Silv., *Solenotus* sp.—bear either short hairs or tubercles on at least a few of the body segments.

The fully grown larvae of *O. arsames*, *O. skianeuros*, *O. trilineata*, *O. euedoreschus* (fig. 1) and *O. gallarum* are very similar to each other and of typical Eulophid form. They are completely without hairs and white in colour with a smooth, shining cuticle. Body segments two to ten inclusive each bear a pair of very small spiracles. The head (fig. 2) is small and transverse, with two prominent ridges on the frons running dorso-ventrally. The antennae, situated below and distal to these ridges, are extremely small and inconspicuous. The mandibles (fig. 3) are simple, being armed with a single, rather blunt tooth. A single pair of palps only (? maxillary) could be detected. The clypeus has a straight, undivided edge and it lies in an almost horizontal plane overlying the mouth which is protruded forwards to form a short snout.

---

*Now at Department of Zoology, The University, Manchester.

Olynx euedoreschus (Walker)

The biology of *O. euedoreschus* is described first, since it was one of the most numerous *Olynx* species in Wytham Wood during the two years in which observations were made.

O. euedoreschus appears to be completely specific to the gall of *Andricus quadrilineatus* Htg., and in Wytham Wood in May 1959, 66 out of 90 mature galls contained *O. euedoreschus* larvae. Galls collected at Otmoor, Oxfordshire by Dr. M. F. Claridge also contained ova of *O. euedoreschus*. Numbers of *O. euedoreschus* bred are given in Table I.

Table I.—*Breeding records of* Olynx *spp.*

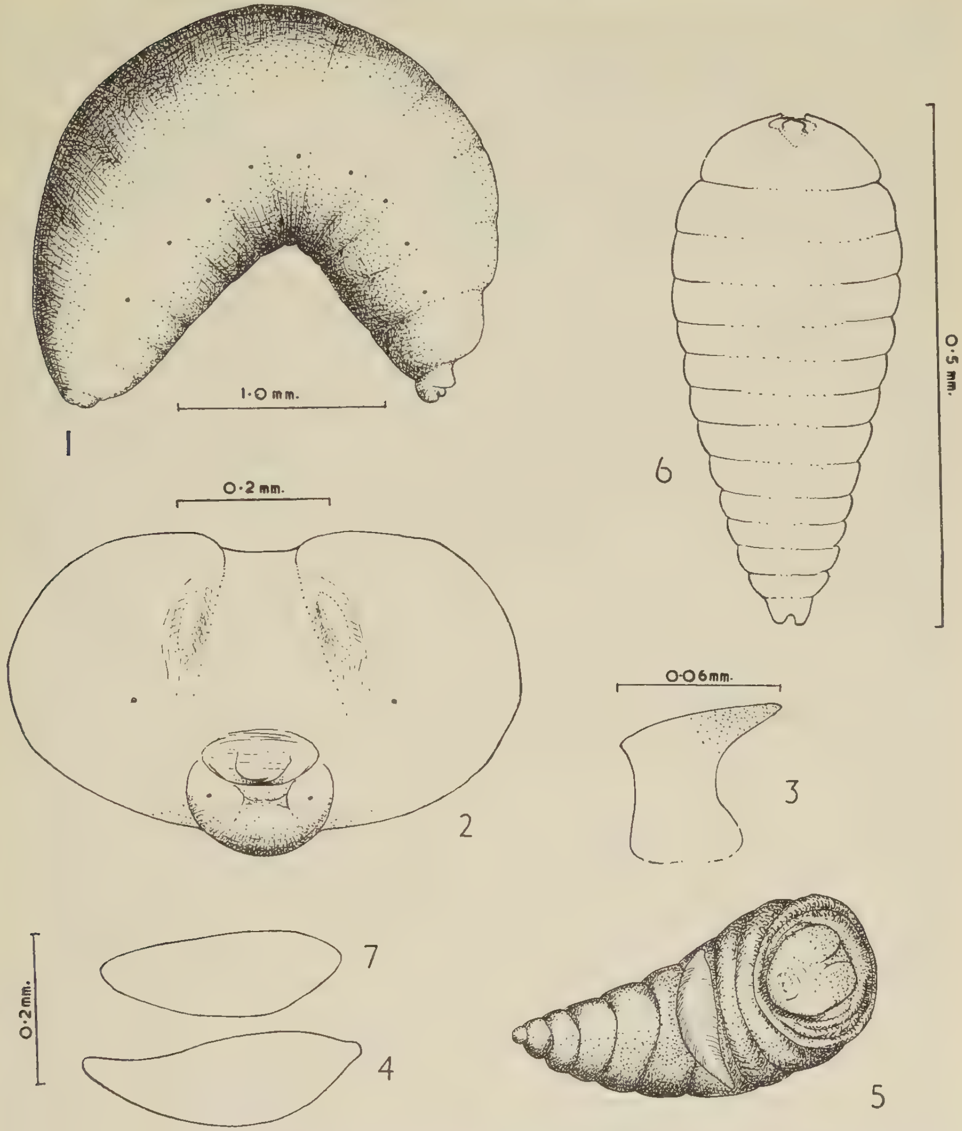
Host galls	*arsames*		*skianeuros*		*gallarum*		*gallarum* f. *pulchra*		*euedoreschus*	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
B. pallida	.	.	453	291	.	.	.	.	.	.
N. quercus-baccarum	2	16	.	.	.	.	.	.	.	.
N. albipes	.	3	.	.	.	.	.	.	.	.
N. n. f. *vesicator*	.	7	.	.	.	.	.	.	.	.
N. q.-b. f. *lenticularis*	.	.	.	.	.	.	2	9	.	.
A. curvator	2	39	.	.	2	.	.	.	.	.
A. inflator	.	1	.	.	.	.	.	.	.	.
A. quadrilineatus	.	1	.	.	.	.	.	.	.	51
A. quercus-ramuli	.	.	.	.	3	12	.	.	.	.
A. ostreus	1	.	.	.	.	.	.	.	.	.

All the specimens bred have been females, as have all those (70) that were captured in the field. The only two males seen are contained in the Oak Survey collection, Hope Department of Entomology, Oxford and in C. G. Thomson's collection, Lund, Sweden. The species probably reproduces by parthenogenesis.

The flight period of *O. euedoreschus* (fig. 8) is synchronised with the time of appearance of its host gall. Galls of *A. quadrilineatus* first appeared on the male catkins on 2nd May, 1958 and 22nd April, 1959. In 1958 the earliest capture of a specimen of *O. euedoreschus* was on 2nd May, and in 1959 on 19th April. The flight period is short and the host galls fall to the ground about three weeks after their first appearance.

Female *O. euedoreschus* were observed flying about the oak trees in a manner characteristic of many gall-inhabiting Chalcidoids. They flew a few millimetres from the peripheral foliage, always facing towards the tree. In front of bunches of male catkins they would hover for a few seconds and usually alight. Only occasionally were they seen to settle on leaves, except during rain showers when several were found sheltering on the undersurfaces. Young male catkins protruding about a centimetre from the bud scales were particularly attractive to searching females. Many females were seen examining these with their antennae, concentrating their investigations just above the bud scales. Sometimes the ovipositor would be thrust down between the scales, and removal of the scales usually revealed the presence of young galls of *A. quadrilineatus*. Young galls on the catkin just above the scales were also drilled and oviposited in, but older galls on the more distal parts of the catkin were largely ignored. A female timed while ovipositing took 81 seconds to complete the act, 34 seconds being taken to pierce the gall wall with its ovipositor.

When *O. euedoreschus* first emerges its ovaries are devoid of mature eggs, and females kept without food die before producing any eggs. In the field, female *O. euedoreschus* were seen to feed on honey-dew on the oak leaves and on some substance



Figs. 1–7.—(1) Fully grown larva of *Olynx euedoreschus* (Walk.), lateral view. (2) Head of fully grown larva of *O. euedoreschus,* front view. (3) Mandible of fully grown larva of *O. euedoreschus.* (4) Egg of *O. euedoreschus.* (5) The same, *in situ* on the larva of *Andricus quadrilineatus* Htg. (6) First instar larva of *O. euedoreschus,* dorsal view (tracheal system omitted). (7) Egg of *O. arsames* (Walk.).

on the male catkins. The maximum number of mature eggs found in a female captured in the field was 64.

The eggs are usually laid singly. The distribution of eggs and first and second instar larvae in 73 galls was as follows : 31 galls contained a single parasite, 3 galls contained two parasites each and 1 gall contained 3 parasites. These cases of superparasitism are probably the result of attack by more than one female. Only one parasite in a gall is able to complete its development.

The position in which the eggs of *O. euedoreschus* are laid in galls of *A. quadrilineatus* is remarkably constant, and this may account for the long time that the ovipositor remains in the gall after it has pierced the gall wall (*antea*). The eggs are always laid on the body of the first or second instar *A. quadrilineatus* larvae, and in 23 out of 25 instances they were found on the ventral surface of the host larva (fig. 5). In this position they cannot be dislodged by movements of the *A. quadrilineatus* larva, which is not paralysed by the female *O. euedoreschus*. Of the remaining two instances, one egg was laid on the side of the thorax of the host larva, and one on the dorsal surface of the abdomen. This site selection has not been noticed by the author in any other gall-inhabiting Chalcidoid. It is probably correlated with the unusual fact that the small host larva is not paralysed but continues to grow for a time, causing its gall also to continue growing.

Galls parasitised by *O. euedoreschus* are of a different texture from those containing healthy *A. quadrilineatus* larvae, being thicker-walled and harder. A simple device was constructed to measure the resistance of the gall wall to penetration by a steel needle. A plastic rod was pivoted in the centre, and to one end was attached a needle. A small metal cup was fitted beneath the needle and halved galls were placed in it with their outer walls uppermost. To the other end of the rod was fixed a Salter Spring Balance which measured tensions of up to 200 grammes. Tension applied to the balance was transmitted to the needle which pressed down on the half gall in the cup. The tension at which the needle pierced the gall wall was taken as a measure of " gall resistance ". The resistances of the walls of galls of *A. quadrilineatus* which contained *O. euedoreschus* eggs or larvae averaged 70 gm. (range 40 gm.–110 gm.) whilst the resistances of those which were unparasitised averaged only 15 gm. (range 10 gm.–25 gm.). The greater resistance of the wall of galls which contained *Olynx* will help to protect the *Olynx* from later attack by other parasites.

The larvae of *O. euedoreschus* grow rapidly, feeding on the bodies of their hosts. First instar *Olynx* larvae were observed piercing the cuticles of their hosts and drawing up the body contents. In 1959 the first eggs of *O. euedoreschus* were found on 24th April, and the first fully grown larvae on 13th May. When the galls fall to the ground the *Olynx* larvae are fully grown. Parasitised galls opened in the winter contained either fully grown *Olynx* larvae, or *Olynx* pupae inside which the adult insects were already fully formed. Seven larvae and eleven pupae were found in 18 galls opened in December, 1958. Adult insects emerged from all the pupae in the following spring. Four of the larvae had pupated by the following October, two had died and the single, living larva was probably destined to pupate the following autumn. Adults quickly emerged during the winter from pupae kept in a warm room. Some other species of Chalcidoid (e.g. *Ormocerus* spp.), which attack early galls, also overwinter as pupae containing fully formed adults, and the habit is evidently an adaptation to secure an early spring emergence coinciding with the bud bursting of the trees and the first gall development of the year. The vast majority of Hymenoptera pass the winter as fully grown larvae.

A single, female *O. euedoreschus* emerged from an *A. quadrilineatus* gall on 30th June, 1958, in the first year of the gall. In the Oak Survey collection are two females labelled as emerging from soil under ground traps on 27th June, 1950 and 25th June, 1951. These females would probably have been unable to reproduce because of the unavailability of suitable host galls. They are of interest in being comparable to the *pulchra* form of *O. gallarum* discussed below. Apart from being rather smaller, they differed in no respect from insects of the spring generation.

Olynx trilineata Mayr

O. trilineata is the rarest of the five British species of *Olynx*. In the British Museum (Nat. Hist.) there are nine female specimens of this species, labelled Epping Forest, Essex, bred from galls of *Andricus fecundator* (Htg.) in March and April, 1939. Niblett (1951) has also bred this species from *A. fecundator* galls. He mentions that on one occasion he had several emerge in the second year of the galls, but the majority of those he has bred have emerged in the third year, while one came out in the fourth year, all in April. I have no certain experience of *O. trilineata*, but a full grown *Olynx* larva, found in a gall of *A. fecundator* from Wytham Wood, was possibly of this species. Mayr (1877) records *O. trilineata* from several types of oak galls on the continent.

O. trilineata must have a summer flight period in order to attack galls of *A. fecundator*, which do not appear until July. Possibly, at least in Britain, it has no spring emergence. The insects reared in March and April were probably " forced ", although the possibility that the species has two generations a year, like *O. gallarum*, must not be overlooked.

Olynx gallarum (Linnaeus) and *Olynx gallarum* f. *pulchra* Mayr

In June, 1958, both sexes of the nominotypical form of *O. gallarum* were obtained from a gall of *Andricus quercus-ramuli* (L.) gathered in Wytham Wood earlier in spring of the same year. Two males were also bred in June, 1958, from galls of *Andricus curvator* Htg. from Wytham Wood. Numbers of bred specimens from galls from Wytham Wood are included in Table I. Specimens of *O. gallarum* bred from *A. quercus-ramuli* galls gathered at Hemel Hempstead, Hertfordshire (*R. B. Benson*) and Woodhall Spa, Lincolnshire (*J. Wield*) and now in the British Museum (Nat. Hist.) were also examined.

The flight period of the nominotypical form is in July in Wytham Wood (fig. 8) and it is the only *Olynx* that was taken in this month. It has been recorded (Askew, 1959) from other localities in August. Since it emerged from *A. quercus-ramuli* and *A. curvator* galls formed in May of the same year, it is obvious that it must also have a spring flight period, but among the many specimens of *Olynx* taken in the spring there were no *O. gallarum*. In July, 1958, a few female *O. gallarum* were observed drilling young spangle galls of *Neuroterus quercus-baccarum* f. *lenticularis* (Oliv.), *N. albipes* f. *laeviusculus* Schenck and *N. numismalis* (Geoff.). On examination of large collections of these galls later in the year, 14 *Olynx* larvae were found in 81 galls of *N. quercus-baccarum* f. *lenticularis* but no *Olynx* larvae were found in spangle galls of the other two species.

Most of the *Olynx* larvae in *N. quercus-baccarum* f. *lenticularis* galls had pupated by September, 1959, and removal of the fully formed adults from some of these pupae revealed them to be *O. pulchra*. Two adult *O. pulchra* (male and female) emerged in September from pupae kept in a heated room and one female emerged the following spring (1960) from a gall of *N. quercus-baccarum* f. *lenticularis* which had overwintered out of doors. Thus the connection between *O. pulchra* and *O. gallarum* was established. The name *O. gallarum* (Linnaeus, 1761) takes precedence over *O. pulchra* (Mayr, 1877).

O. gallarum f. *pulchra* has the same spring flight period (fig. 8) as *O. arsames*, *O. skianeuros* and *O. euedoreschus*. On 3rd May, 1958 a female was found drilling into a gall of *A. curvator*. As mentioned above, the nominotypical form has been bred from galls of this species.

Olynx arsames (Walker)

O. arsames was bred from galls of *Neuroterus quercus-baccarum* (L.), *N. numismalis* f. *vesicator* (Schlecht.), *N. albipes* (Schenck), *Andricus quadrilineatus* Htg., *A. curvator* Htg., *A. ostreus* (Htg.) and *A. inflator* Htg. collected in Wytham Wood. Breeding records are contained in Table I, which also includes specimens bred from galls of *A. curvator* collected at Coldstream, Berwickshire (2 females); Cornhill-on-Tweed, Northumberland (4 females); Gosforth, Northumberland (2 females); Cothill, Berkshire (1 female); and Jersey, Channel Islands (1 female), and in the Oak Survey collection (6 females). Its pupae were found in galls of *A. curvator* from Kinlochmoidart, Inverness-shire, and in galls of *A. inflator* from Cothill, Berkshire. The galls most frequently attacked by *O. arsames* are those of *A. curvator* and *N. quercus-baccarum.*

Galls of *N. quercus-baccarum* grow either on oak leaves or male catkins, and in 1959 numbers of *Olynx* larvae in galls from these two situations were compared. *O. arsames* is the only species of *Olynx* associated with these galls. Of 128 galls growing on catkins, 17 (13 per cent.) contained *Olynx* larvae, while 29 out of 72 (40 per cent.) galls growing on leaves and examined at the same time as the catkin galls contained *Olynx.* The catkin galls fall to the ground in May but the leaf galls remain on the tree until the leaves themselves fall in autumn and, owing to the attacks of later parasites, the percentage of *Olynx* decreases in the leaf galls throughout the summer. A collection of 51 leaf galls of *N. quercus-baccarum* made in 1959, after the catkins had fallen, included only 5 (10 per cent.) which contained *Olynx.* Thus the species would seem to have a better chance of survival in the catkin galls than in the leaf galls. Why then does the species attack more leaf galls than catkin galls? Galls of *N. quercus-baccarum* occur in large numbers on the catkins of only relatively few trees, whereas the leaf galls are more widely distributed, occuring even on immature trees which do not bear catkins. Further, galls of *A. curvator* grow on the leaves or leaf petioles, and galls of *N. numismalis* f. *vesicator* are confined to the leaves. Probably so many more host galls are discovered by searching leaves than by searching catkins that the greater mortality of *O. arsames* in leaf galls is offset by the greater number of hosts found on the leaves.

Observations made on a single catkin-bearing tree during 7 days in April and May, 1959, confirm that *O. arsames* searches leaves more than it does catkins, even when, as in the case of this tree, the catkins bear considerable numbers of *N. quercus-baccarum* galls. Altogether only 11 female *O. arsames* were found searching catkins during this period, while 43 were found searching leaves, although those insects on the catkins are more easily seen. During May, 1958, female *O. arsames* were observed in Wytham Wood drilling galls of *A. curvator*, *N. quercus-baccarum* and *N. aprilinus* (Giraud). No *Olynx* have been bred from the last mentioned gall.

The host gall list of *O. arsames* includes all the species of Cynipid that have galls forming on the oak leaves during its flight period.

The males of *O. arsames*, as of *O. euedoreschus*, are relatively scarce. The author has bred 4 male and 67 female *O. arsames*, and captured in the field 4 males and 165 females.

As with *O. euedoreschus*, female *O. arsames* on first emerging have immature ovaries and they require nourishment to promote their development. Females in the field were observed feeding on the surface of oak leaves (possibly on honey-dew), and others were beaten from flowering sallow and blackthorn. Only a single adult *O. arsames* emerges from each parasitised gall, and on no occasion was more than one parasite found in a gall. The host larvae are not paralysed by ovipositing female *O. arsames* and the eggs are laid on the ventral surfaces of the first or second instar gall forming larvae, in a similar position to the eggs of *O. euedoreschus* on the larvae of *A. quadrilineatus.*

Galls of *N. quercus-baccarum* containing *Olynx* larvae are of a different texture from galls containing only the gall maker, and this is another point of similarity with *O. euedoreschus.* The galls containing *Olynx* are smaller and have thicker walls than unparasitised galls, and they have a hard layer of tissue surrounding the larval chamber. The mean diameter of 10 catkin galls of *N. quercus-baccarum* containing the gall maker was 7·4 mm. (limits 6·0 mm. and 9·3 mm.), and a gall of diameter 7·9 mm. had a wall 1·5 mm. thick. In contrast, the mean diameter of 10 catkin galls containing *Olynx* was only 4·7 mm. (limits 4·0 mm. and 5·5 mm.), and a gall of diameter 4·9 mm. had a wall 2·0 mm. thick. The same feature is even more noticeable with leaf galls of *N. quercus-baccarum.* The mean diameter of 10 leaf galls containing the healthy gall maker was 8·8 mm. (limits 6·5 mm. and 10·8 mm.), but the mean

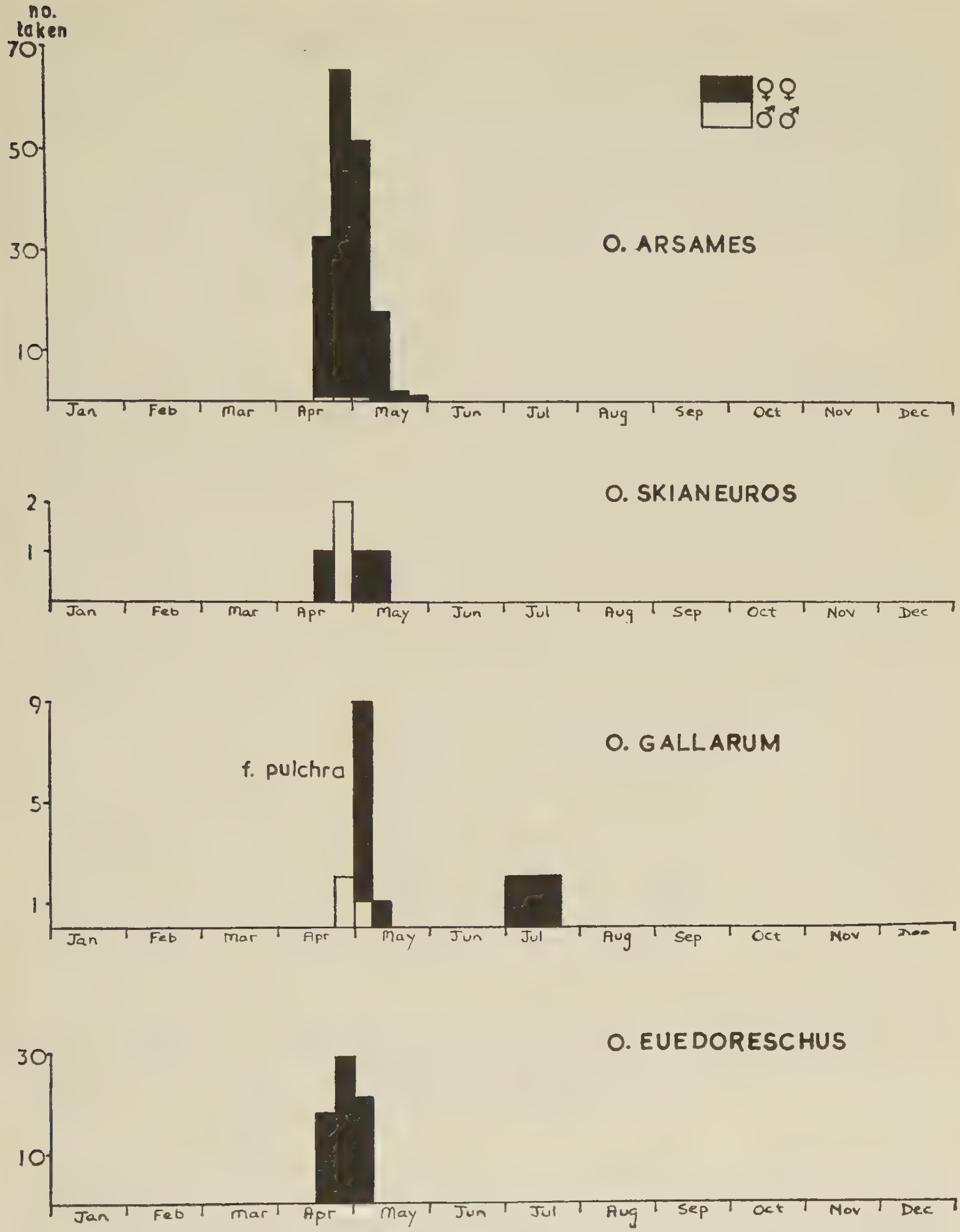


FIG. 8.—The flight periods of *Olynx arsames* (Walk.), *O. skianeuros* (Ratz.), *O. gallarum* (L.) and *O. euedoreschus* (Walk.).

diameter of 10 leaf galls containing *Olynx* was only 4·5 mm. (limits 2·9 mm. and 5·6 mm.).

The resistances of the walls of unparasitised galls of *N. quercus-baccarum* averaged 15 gm. (range 10 gm.–20 gm.) whilst the resistances of those which contained *O. arsames* eggs or larvae averaged 60 gm. (range 25 gm.–90 gm.). Galls from which *N. quercus-baccarum* have emerged soon turn very soft and they quickly rot. Those containing *Olynx* retain their form. The increased hardness of galls containing *Olynx* probably serves, in the case of leaf galls, to protect the parasite from attacks later in the year by other Chalcids, and in the case of catkin galls, to prevent the gall decaying on the ground. The presence of *O. arsames* apparently has no effect on the form of the galls of its other hosts.

The *Olynx* larvae grow very rapidly, and a prepupa was found in a gall of *A. curvator* as early as 25th June, 1958. As with the other species, a proportion of the larvae pass two, and and some possibly more, winters in the gall. In the winter of 1958–59, four larvae and five pupae were found in galls of *A. curvator*. The pupae, even as early as September, contained fully formed adults which emerged the following spring.

Olynx skianeuros (Ratzeburg)

O. skianeuros is a specific parasite of *Biorhiza pallida* (Oliv.) galls. It is widespread in Britain, and the author has bred it from galls collected at Rosthwaite, Cumberland; Arrochar, Dunbartonshire; Hell Coppice, Buckinghamshire; Coldstream, Berwickshire; Neville's Cross, Durham; Oxford and Wytham Wood. Galls from Glen Borrodale, Argyllshire, contained pupae of this species. In addition, specimens bred from *B. pallida* galls from the following localities have been examined in the British Museum (Nat. Hist.): Scarborough, Yorkshire (*B. R. Lucas*); Limpsfield and Gomshall, Surrey (*M. Niblett*); Worcester Park, Surrey (*R. D. Eady*) and Hampstead, London (*K. G. Blair*). Numbers of specimens bred by the author (all localities) are included in Table I. It is noteworthy that the sex ratio of this species favours the males, and thus contrasts with the sex ratios of the other species.

The flight period of *O. skianeuros* (fig. 8) coincides with the appearance of its host galls on the trees. In 1959 the first specimen was caught on 22nd April, five days after the first young gall of *B. pallida* had been found.

In the two years of study only five specimens of *O. skianeuros* were taken in the field and this figure is out of all proportion to the large number bred, which suggests that this species usually flies high in the canopy, where the galls of *B. pallida* are most numerous. One female was beaten from blackthorn flowers.

The gall of *B. pallida* grows rapidly to a large size, and only for a few days after its first appearance is it possible for the *Olynx* to penetrate with its ovipositor to all of the larval chambers. A layer of spongy tissue surrounds the peripheral cells of a fully grown gall to a depth of 4 or 5 mm., whilst the ovipositor of a large female *O. skianeuros* is only about 1·4 mm. long. Even so, cells right in the centres of galls just as frequently contain *Olynx* larvae as the more peripheral cells, indicating that the galls are attacked at a very early stage of development when the host larvae are very small. The ovipositor of a female *O. skianeuros* is slightly more exserted than in the other species, and relatively longer, presumably as an adaptation to the larger size of its host gall.

As with the other *Olynx* species, the larvae grow rapidly, and in 1959 nearly all were fully grown by mid-May. Galls of the previous spring kept indoors and opened in the winter of 1958–59 contained 92 larvae and 33 pupae of *O. skianeuros*. The pupae contained fully formed adults which emerged during the following spring when kept out of doors, but those retained in a heated room emerged within a few weeks. The larvae did not change their state until the following autumn when 12 out of 15 had pupated.

SEASONAL COLOUR FORMS IN THE CHALCIDOIDEA

Gradwell (1958) has shown that *Comedo* (= *Eulophus*) *larvarum* (L.) (Eulophidae) is dimorphic. In spring the species is represented by form *nigribasis* Gradwell, which has a wholly metallic gaster. This form gives rise both to insects of the nominotypical form, characterised by a pale area at the base of the gaster, later in the same year, and to insects of form *nigribasis* the following spring. Morphological differences between the forms are very slight. This example differs from the next in that the alternation of forms is only partial, the spring form being capable of producing some insects the following spring without the intervention of the summer form. The primary factor which determines whether a given insect becomes adult in the summer, or overwinters to produce form *nigribasis*, would appear to be genetic, since the offspring of a single *nigribasis* female may become adult both in the summer and in the following spring, even though apparently exposed to the same conditions.

The difference between *Olynx gallarum* and *O. gallarum* f. *pulchra* is again largely one of colour. The overwintering form (*pulchra*) is generally darker than the nominotypical summer form and it has a dark line, not found in the nominotypical form, on the flexor aspects of the middle tibiae. The differences between the forms in both these examples have been sufficiently marked to cause the forms, in the past, to be given specific status. They emphasise the need for combined biological and taxonomic studies of the Chalcidoidea.

Recently, Murakami (1960) has discovered a seasonal dimorphism in two species of Encyrtidae. Females of *Anagyrus schönherri* (Westwood) and both sexes of *Aphycus albicornis* Timberlake are considerably darker in colour in the overwintering generation than in the summer generation.

Marchal (1931, 1936) showed that adults of the overwintering generation of *Trichogramma cacoeciae* Marchal are rather darker in colour than summer generation insects.

In all these examples it is the overwintering spring generation which has the darker pigmentation. A similar situation has been noted by the author with respect to *Torymus auratus* (Fourc.), *T. cingulatus* Nees and *T. nigricornis* Boh., in all of which insects of the naturally bred overwintering generation are of a duller green colour, and are more extensively and darkly pigmented on the legs, than are insects of the summer generation, which have not overwintered. However, if overwintering larvae are brought indoors in early winter and kept in the warmth of a laboratory, they quickly produce adults which have the coloration characteristic of non-overwintering insects. This agrees with the findings of Flanders (1931), on *Trichogramma minutum* Riley ; he showed that the amount of dark pigmentation is determined by the duration of exposure to low temperatures during the early pupal period.

SUMMARY

1. The immature stages of *Olynx* are described, and the biologies of *O. euedoreschus* (Walker), *O. trilineata* Mayr, *O. gallarum* (L.), *O. arsames* (Walker) and *O. skianeuros* (Ratzeburg) in Wytham Wood, Berkshire are considered.

2. *O. gallarum* is dimorphic. The nominotypical form is in flight in summer and it gives rise to form *pulchra* Mayr, in flight in spring.

3. *O. euedoreschus* is a specific parasite of galls of *Andricus quadrilineatus* Htg., *O. trilineata* of galls of *A. fecundator* (Htg.), and *O. skianeuros* of galls of *Biorhiza pallida* (Oliv.). *O. gallarum* emerged mainly from galls of *A. quercus-ramuli* (L.), but also from galls of *A. curvator* Htg. ; *O. gallarum* f. *pulchra* emerged from galls of *Neuroterus quercus-baccarum* f. *lenticularis* (Oliv.). *O. arsames* was bred from galls of *N. quercus-baccarum* (L.), *N. numismalis* f. *vesicator* (Schlecht.), *N. albipes* (Schenck), *A. quadrilineatus*, *A. curvator*, *A. ostreus* (Htg.) and *A. inflator* Htg.

4. All the species have a brief flight period which coincides with the short time during which their host galls are on the trees or in a suitable condition for attacking.

5. The *Olynx* larvae feed only on the larvae of the gall makers. It is usual for only one egg to be laid on each host larva, and the habit of depositing the egg on the ventral surface of the unparalysed host larva, observed in *O. euedoreschus* and *O. arsames*, may occur throughout the genus.

6. *O. euedoreschus*, and sometimes *O. arsames*, have been shown to cause their host galls to become harder and less easily penetrable by other parasites.

7. *O. skianeuros*, *O. arsames*, *O. gallarum* f. *pulchra* and *O. euedoreschus* spend the winter before their emergence, which may be delayed a year or more, as pupae which contain fully formed adults. This is believed to be an adaptation to secure a spring emergence which coincides with the bud bursting of the trees and the first gall development of the year.

8. On morphological considerations, *O. gallarum*, *O. trilineata* and *O. euedoreschus* have been placed (Askew, 1959) in the same species group. Biologically, also, this group of species share an important character. As demonstrated above, *O. gallarum* has both a spring and a summer flight period. *O. euedoreschus* apparently also has a very slight summer emergence, although primarily a single brooded species, and *O. trilineata* must have a summer flight period in order to attack galls of *Andricus fecundator*, which do not appear until July. In contrast to the tendency towards a summer flight period in the *O. gallarum* species group, there is only a spring flight period in *O. arsames* and *O. skianeuros*.

9. Seasonal colour differences in the Chalcidoidea are discussed. Adults of the overwintering generations of a number of species are of darker coloration than adults of summer generations.

ACKNOWLEDGMENTS

This paper was completed whilst in receipt of a research grant from the Department of Scientific and Industrial Research.

I am indebted to the following gentlemen for helpful criticism and discussion during the course of this work: Professor G. C. Varley, Dr. M. W. R. de V. Graham, Dr. M. F. Claridge and Mr. G. R. Gradwell. I also wish to thank Mr. J. F. Perkins and Mr. G. J. Kerrich, British Museum (Nat. Hist.), and Professor C. H. Lindroth, Universitets Zoologiska Institution, Lund, for making it possible to examine specimens in their care.

REFERENCES

ASKEW, R. R., 1959, A revision of the British species of the genus *Olynx* Förster (Hym., Eulophidae). *Ent. mon. Mag.* **95** : 49–57.

FLANDERS, S. E., 1931, The temperature relationships of *Trichogramma minutum* as a basis for racial segregation. *Hilgardia* **5** : 395–406.

GRADWELL, G. R., 1958, *Eulophus nigribasis* Gradwell (Hym., Chalcidoidea) the overwintering form of *E. larvarum* (L.). *Ent. mon. Mag.* **94** : 234–5.

LABOULBÈNE, A., 1877, Liste des éclosions d'insectes observées par le Dr. Joseph-Etienne Giraud, membre honoraire. *Ann. Soc. ent. Fr.* **7** : 397–436.

LINNAEUS, C., 1761, *Fauna Suecica* (*edit. altera*) : 409.

MARCHAL, P., 1931, Le microptérisme et le dimorphisme saisonnier chez les Trichogrammes. *C.R. Acad. Sci. Paris* **192** : 316–18.

—— 1936, Recherches sur la biologie et le développement des Hyménoptères parasites. Les Trichogrammes. *Ann. Epiphyt.* **2** : 447–550.

MAYR, G., 1877, Die Chalcidier-Gattung *Olinx*. *Verh. k. k. zool.-bot. Ges. Wien* **27** : 155–164.

MURAKAMI, Y., 1960, Seasonal dimorphism in the Encyrtidae (Hymenoptera, Chalcidoidea). *Acta Hymenopterologica* **1** : 199–204.

NIBLETT, M., 1951, Some notes on *Andricus fecundator* Htg. (Cynipidae, Hym.). *Proc. S. Lond. ent. nat. Hist. Soc.* **1951–52** : 134–6.

PARKER, H. L., 1924, Récherches sur les formes post-embryonnaires des Chalcidiens. *Ann. Soc. ent. Fr.* **93** : 261–379.

OBSERVATIONS ON NOCTURNAL FLIGHT ACTIVITY IN SOME AFRICAN CULICIDAE (DIPTERA)

By Philip S. Corbet and A. J. Haddow

(*East African Virus Research Institute, Entebbe, Uganda*)

In 1958, a series of mercury-vapour light-trap catches was made at Entebbe, Uganda, in order to test the efficiency of different designs of trap and of various types of killing agent. This series provided information also on the nocturnal activity of Tabanidae and Culicidae. Our observations on the Tabanidae have been recorded elsewhere (Haddow and Corbet, 1960); those on the Culicidae form the subject of the present paper. The trap, the methods of collection and the site have already been described in the account of the Tabanidae, and only a few details need be repeated here.

The trap stood about 3 feet above the ground in a shaded garden some 300 feet above, and three-quarters to one mile from, Lake Victoria. The surroundings comprised the Institute compound, with close-cut lawns and well-grown trees, African plantations, mainly of banana, cassava and coffee, and large lakeside swamps of grass and papyrus, adjoining part of which is a narrow belt of swamp-forest, about half a mile away from the trap site.

The total series consisted of 55 all-night catches made between 17th June and 12th September. This included 23 catches (22nd July to 11th August) in which the contents of the trap were removed at hourly intervals. After we had confirmed (from two 24-hour catches) that no mosquitoes were being caught during the daytime, the trap was run for 14 hours only, from an hour before sunset until an hour after sunrise, this period being designated as 17.00–07.00 " catch-time ".

The mosquitoes caught in the total series and the timed series, respectively, are listed in Table I.

The uncertain determinations result from the material having been collected in alcohol, since mosquitoes obtained in this way are often difficult to identify. The specimens assigned to a species near *Uranotaenia pallidocephala* can be distinguished from the type form only by differences in the tibial chaetotaxy of the male. Therefore the status of the females in the present series remains equivocal.

Most of the species caught are typically encountered in the belt of swamp-forest nearby, but *Mansonia fuscopennata* and the two species of *Mansonioides* commonly bite also over open ground at night. Furthermore it is known that, amongst the species of *Mansonia* represented here, those associated mainly with forest are avian feeders (Williams, Weitz and McClelland, 1958), whereas the other three feed on a variety of hosts including man (Gillett, 1946; Haddow and Dick, 1948; Haddow *et al.*, 1951; Lumsden, 1956; McClelland and Weitz, 1960).

These differences appear to be reflected in the sex ratios of the two types of mosquito. In the forest species combined, females made up only 18·9 per cent. of the total of 175 mosquitoes caught, but in the three open-ground species females comprised 86·2 per cent. of 1125. Thus there is a possibility that, in a certain site, the sex ratio of a species may reflect its feeding habits.

These results indicate that males of some sylvan mosquitoes may show considerable activity outside forest at night. It should, however, be remarked that, in the present records, the excess of males in the combined catches of the forest species is determined largely by *M. metallica* and *M. fraseri*, males of which commonly rest outside forest during the day. Thus it must be noted that the males which are

Table I.—*Mosquitoes caught at mercury-vapour light, Entebbe, Uganda*

Species	Total series		Timed series	
	Males	Females	Males	Females
Anopheles (*Myzomyia*) *marshalli* Theo.?	1	.	.	.
gambiae Giles	1	.	.	.
Uranotaenia pallidocephala Theo.	.	3	.	.
sp. nr. *pallidocephala* Theo.	3	.	.	.
nigromaculata Edw.	1	.	.	.
sp.	2	1	2	1
Ficalbia (*Mimomyia*) *femorata* Edw.	.	4	.	.
sp.	.	1	.	.
Mansonia (*Coquillettidia*) *metallica* Theo.	81	15	20	4
pseudoconopas Theo.	1	.	.	.
maculipennis Theo.	1	.	.	.
fuscopennata Theo.	148	945	42	196
aurites Theo. group	8	3	.	.
fraseri Theo.	26	8	6	5
(*Mansonioides*) *africana* Theo.	1	7	1	3
uniformis Theo.	5	17	.	4
sp.	1	1	.	.
Aëdes (*Neomelanoconion*) *circumluteolus* Theo.	1	.	.	.
sp.	1	.	.	.
Culex (*Lutzia*) *tigripes* Grp. and C.	2	.	.	.
(*Neoculex*) *rubinotus* Theo.	2	.		
insignis Cart.	3	.	.	.
(*Culex*) *annulioris* Theo.	2	.	.	
argenteopunctatus Ventr.	.	1	.	.
univittatus Theo. var. *neavei* Theo.	2	.	.	.
pipiens L.	1	.	.	.
quasiguiarti Theo.?	1	.	.	.
spp.	3	2	2	2
Totals	298	1008	73	215

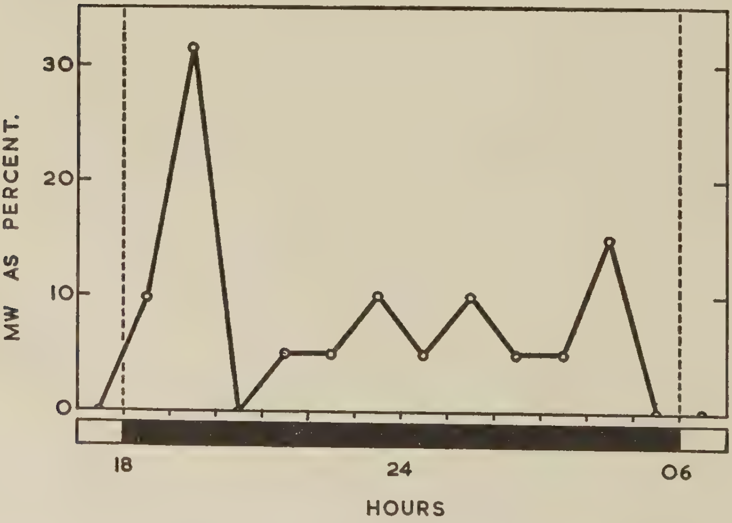


Fig. 1.—Flight activity curve for males of *Mansonia metallica*. *Ordinate :* Williams' mean (M_w) expressed as per cent. (*see* Haddow, 1960).

active by night in open situations have not necessarily left the forest at, or after sunset.

Only two species were caught in numbers sufficient to show their patterns of flight activity (see Table II). These were *M. metallica* (males) and *M. fuscopennata* (both sexes) (*see* figs. 1 and 2). In males of both species, there was a marked peak of activity in the second hour after sunset (19–20 hours), and indications of a much smaller peak about two hours before sunrise (02–05 hours). In females of *M. fuscopennata*, the pattern was different (fig. 2, *a*) : activity rose gradually from sunset onwards to reach a clear peak in the third hour before sunrise (03–04 hours). It is interesting to note that in the tabanid, *Tabanus thoracinus* Pal. de Beauv., males and females are also active at different times of night (Haddow and Corbet, *loc. cit.*), although in *T. thoracinus* it is the females, instead of the males, which are most active during the earlier part of the night.

TABLE II.—*Catches of mosquitoes at mercury-vapour light, Entebbe, Uganda*

M, male ; *F*, female. Williams' mean (M_W) (*see* Haddow, 1960) has been multiplied by 100 to give integer numbers

	Hours "catch time"														
	17–18	18–19	19–20	20–21	21–22	22–23	23–24	00–01	01–02	02–03	03–04	04–05	05–06	06–07	Totals
M. metallica :															
M, Totals	.	3	5	.	1	1	2	1	2	1	1	3	.	.	20
100 M_W	.	62	198	.	30	30	62	30	62	30	30	94	.	.	—
F, Totals	.	.	1	1	1	.	.	.	.	.	1	.	.	.	4
M. fuscopennata :															
M, Totals	1	4	11	8	4	2	3	1	.	3	3	2	.	.	42
100 M_W	30	128	358	242	128	62	81	30	.	81	81	62	.	.	—
F, Totals	1	5	13	10	12	16	11	14	19	22	38	26	8	1	196
100 M_W	30	161	364	302	348	409	358	469	560	607	1170	714	227	30	—
M. fraseri :															
M, Totals	.	.	.	.	1	.	.	.	1	.	3	1	.	.	6
F, Totals	.	.	.	.	.	.	.	.	.	1	1	1	2	.	5
M. africana :															
M, Totals	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
F, Totals	.	.	.	.	.	.	.	.	.	1	2	.	.	.	3
M. uniformis :															
F, Totals	.	.	.	.	.	.	.	1	1	.	2	.	.	.	4

At present little attempt can be made to rationalise these findings in terms of other cyclical activities. The possible effects of an emergence rhythm on flight activity were investigated by recording the degree of rotation of the male hypopygia. In both *M. metallica* and *M. fuscopennata*, a small proportion (17–20 per cent.) of those caught had incompletely-rotated hypopygia, indicating that they had probably emerged within the previous 24 hours, but the occurrence of such males was not associated significantly with one period of the night. The age of females was not determined, beyond its being noted that the great majority were without visible blood or eggs in the abdomen, and that some female *M. fuscopennata* bore hydrachnid mites, thereby showing that they were almost certainly nulliparous (Gillett, 1957 ; Corbet, 1960).

The pattern of flight activity of female *M. fuscopennata* closely resembles that of oviposition activity (fig. 2, *b*), as recorded in the laboratory by Haddow and Gillett (1958). Nevertheless, as females exhibiting this flight activity were on the whole not gravid, and as some at any rate were nulliparous, it cannot be postulated that such individuals were either seeking, or returning from, oviposition sites. Rather would it seem that, as suggested by Mattingly (1949), certain times in the diel are associated

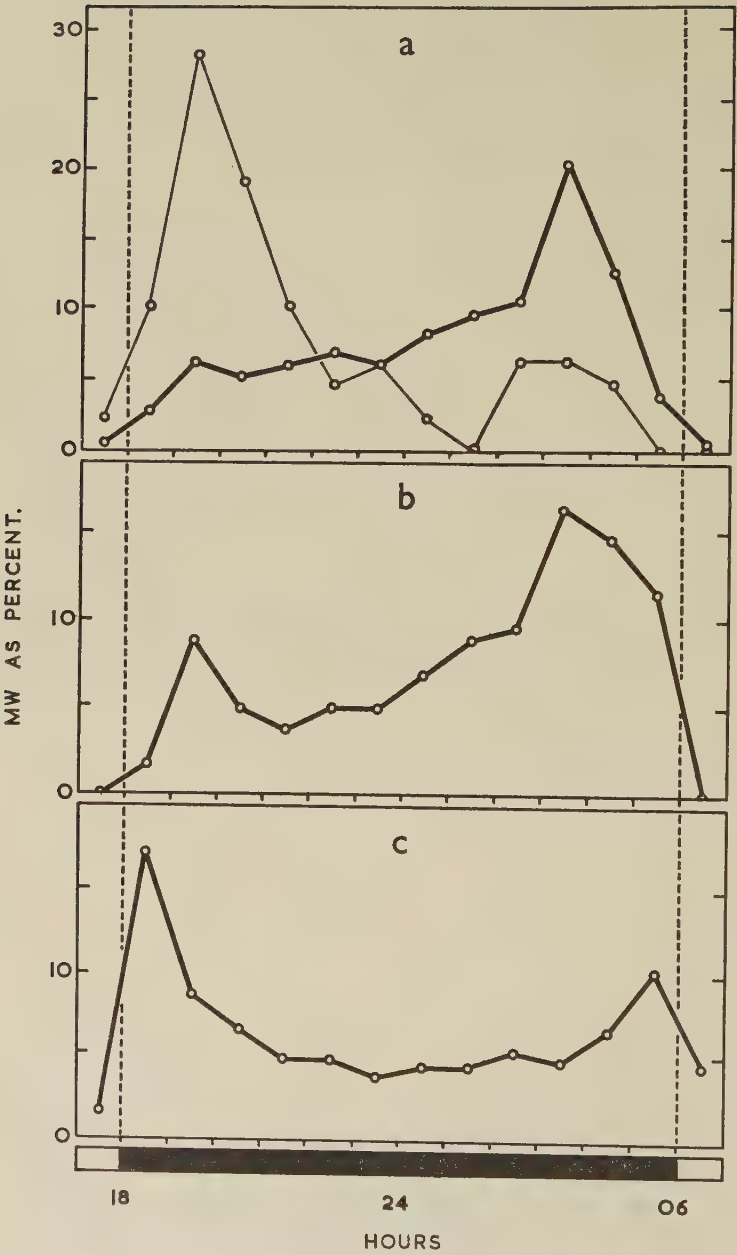


FIG. 2.—*Mansonia fuscopennata.* Activity cycles: (*a*) flight activity (*thin line,* males; *heavy line,* females); (*b*) oviposition activity; (*c*) biting activity.

Data for (*b*) and (*c*) are from Haddow and Gillett (1958).

The period 07–17 hrs, when activity is very low, has been omitted. Ordinates as in fig. 1. To facilitate comparison the highest mean values for females have been adjusted to the same height.

with increased activity, which in this case may find expression either in flight or oviposition, depending on the current physiological condition of the females concerned. That the pattern of female flight activity does not resemble that of biting activity (Haddow, 1956) (fig. 2, *c*) should, however, caution against too wide an application of this principle. Nor should it be forgotten that attempts to rationalise different biological activities in terms of each other are strictly limited by the selectiveness of the methods used to discern those activities. If, as is probable, freshly-fed female mosquitoes usually rest until ready to oviposit, then it is clear that observations on female flight activity can only refer to that limited episode in adult life which lies between either emergence or oviposition, and the acquisition of a blood meal.

Acknowledgments

We wish to thank Mrs. E. C. C. van Someren for identifying some of the mosquitoes, and Mr. G. A. H. McClelland for help in some of the later catches.

Summary

Catches in a mercury-vapour light-trap, sited about half a mile away from forest, have provided data on nocturnal flight activity in some East African mosquitoes.

Males predominated in catches of species typically found in the forest, whereas females outnumbered males in catches of species known also to bite over open ground at night.

In *Mansonia fuscopennata* the patterns of flight activity of males and females differ greatly. The males are most active in the second hour after sunset, and the females in the third hour before sunrise.

The close resemblance between patterns of female flight and oviposition activity in this species is noted and briefly discussed. It is pointed out that observations on female flight activity may refer only to a limited episode in adult life.

References

Corbet, P. S., 1960, Recognition of nulliparous mosquitoes without dissection. *Nature, Lond.* **187** : 525–6.

Gillett, J. D., 1946, Notes on the subgenus *Coquillettidia* Dyar (Diptera : Culicidae). *Bull. ent. Res.* **36** : 425–38.

—— 1957, Age analysis of the biting-cycle of the mosquito *Taeniorhynchus* (*Mansonioides*) *africanus* Theobald, based on the presence of parasitic mites. *Ann. trop. Med. Parasit.* **51** : 151–8.

Haddow, A. J., 1956, Rhythmic biting activity of certain East African mosquitoes. *Nature, Lond.* **177** : 531–2.

—— 1960, Studies on the biting habits and medical importance of East African mosquitos in the genus *Aëdes*. I. Subgenera *Aëdimorphus*, *Banksinella* and *Dunnius*. *Bull. ent. Res.* **50** : 759–79.

—— and Corbet, P. S., 1960, Observations on nocturnal activity in some African Tabanidae (Diptera). *Proc. R. ent. Soc. Lond.* (A) **35** : 1–5.

—— and Dick, G. W. A., 1948, Catches of biting Diptera in Uganda, with anaesthetized monkeys as bait. *Ann. trop. Med. Parasit.* **42** : 271–7.

—— and Gillett, J. D., 1958, Laboratory observations on the oviposition-cycle in the mosquito *Taeniorhynchus* (*Coquillettidia*) *fuscopennatus* Theobald. *Ann. trop. Med. Parasit.* **52** : 320–5.

—— van Someren, E. C. C., Lumsden, W. H. R., Harper, J. O. and Gillett, J. D., 1951, The mosquitoes of Bwamba County, Uganda. VIII. Records of occurrence, behaviour and habitat. *Bull. ent. Res.* **42** : 207–38.

Lumsden, W. H. R., 1956, Arthropods attacking domestic animals. *Ann. Rep. E.A. Virus Res. Inst.* **6** (1955–56) : 44–45. Nairobi (Govt. Printer).

Mattingly, P. F., 1949, Studies on West African forest mosquitoes. Part II. The less commonly occurring species. *Bull. ent. Res.* **40** : 387–402.

McClelland, G. A. H. and Weitz, B., 1960, Further observations on the natural hosts of three species of *Mansonia* Blanchard (Diptera : Culicidae) in Uganda. *Ann. trop. Med. Parasit.* **54** : 300–4.

Williams, M. C., Weitz, B. and McClelland, G. A. H., 1958, Natural hosts of some species of *Taeniorhynchus* Lynch Arribalzaga (Diptera : Culicidae) collected in Uganda, as determined by the precipitin test. *Ann. trop. Med. Parasit.* **52** : 186–90.

THE FUNCTION OF HAGEMANN'S ORGAN IN *CORIXA PUNCTATA* (ILLIG.) (HEMIPTERA : CORIXIDAE)

By Edward J. Popham

(*Department of Zoology, University of Manchester*)

In 1910, Hagemann described a specialised sense organ situated immediately in front of the posterior thoracic spiracles of *Corixa punctata* (Illig.). This organ consists of a membrane (fig. 1, *M.*) and a clubbed process (fig. 1, *CP*). Hagemann suggested that the membrane and associated structures had an auditory function and that the clubbed process functioned as do dipteran halteres. His simple experiments to test these hypotheses are, on his own admission, inconclusive. The function of the organ therefore needs reinvestigation and it is with this matter that this paper is concerned.

Techniques

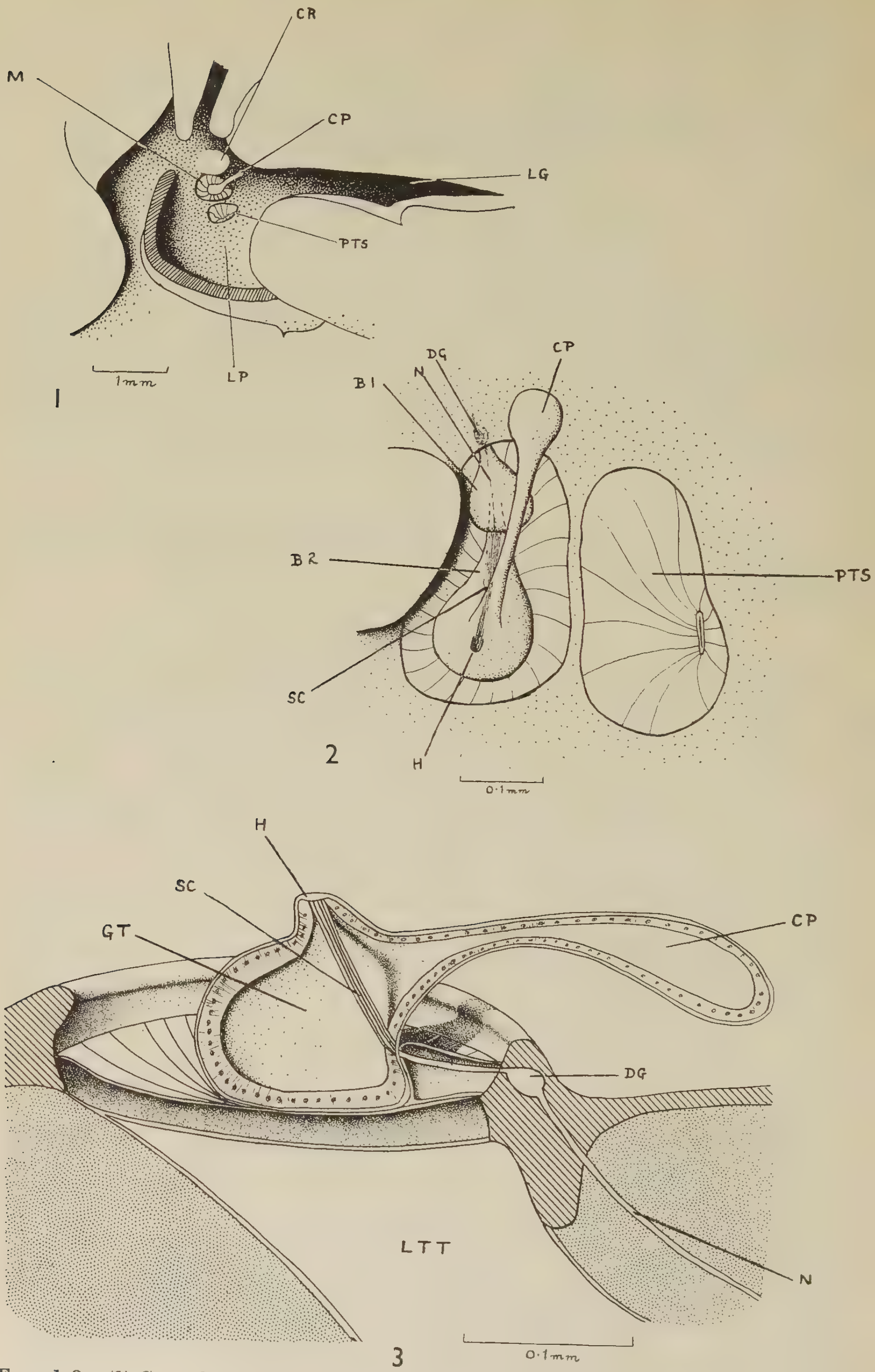
The organ has been studied from dissections, stained preparations of whole mounts and celloidin sections, 20 to 100μ thick, of Zenker fixed material stained with Haemotoxylin or Masson in the usual way.

Hagemann's Organ (figs. 1–3)

The thoracic segments of *Corixa punctata* slope forwards. The anterior thoracic spiracles are placed latero-ventrally between the pro- and pterothorax and are protected by a rectangular-shaped process on the posterior prothoracic margin. The dorsally situated posterior thoracic spiracles are situated lateral to the wing bases in a lateral pouch (fig. 1, *LP*) between the tergal and pleural sclerites. The pouch is normally closed dorsally, when the hemi-elytron is flexed over the abdomen. On the inner wall of this lateral pouch, Hagemann's organ is situated. As Hagemann's original description of the organ is reasonably accurate, it is sufficient to summarise the general features of the organ in order to explain its function.

Immediately behind the base of the front wings is a cuticular ridge (fig. 1, *CR*), which in section is shaped like a geological escarpment, the more vertical face being posterior. Behind this ridge is an oval membrane (fig. 1, *M*) joined to the body wall by a rim of hard cuticle. The lateral tracheal trunk (fig. 3, *LTT*) runs close to the body wall at this point and the membrane separates the tracheal lumen from the cavity of the lateral pouch. The membrane is composed of two sheets of cuticle, each secreted by a layer of squamous cells. The outer cuticular sheet is pleated into radial folds, which mutually overlap in a clockwise direction on the right side of the insect and anti-clockwise on the left, one organ being the mirror image of the other.

Lateral to the dorsal third of the membrane is a vertical flask shaped structure (fig. 2, *B*1), which is joined to the neck of a similar structure (fig. 2, *B*2) lying ventral to the first. These two structures are known as " the base ". Medially the bulbs are in contact with the membrane. The second flask lies lateral to the membrane centre (fig. 3). Ventro-laterally, the second bulb bears a small rectangular hump (figs. 2 and 3, *H*). A number of scolophores are inserted along the junction of the outer and ventral walls of this hump and originate along the outer edge of the junction of the two flask shaped structures (*B*1 and *B*2) (fig. 3, *SC*). These scolophores (fig. 3, *SC*) are innervated from the mesothoracic ganglion *via* a small dorsal ganglion (figs. 2 and 3, *DG*) situated mesad to the dorsal edge of the membrane. The ventral flask-shaped structure (*B*2) also bears the long dorsally directed clubbed process



FIGS. 1–3.—(1) General view of the lateral pouch of *Corixa punctata* (Illig.), part of the lateral wall having been removed. (2–3) Hagemann's organ: (2) general view; (3) transverse section.

(figs. 1, 2 and 3, *CP*), which is inclined backwards at an angle of 30 degrees, the clubbed end lying in the mouth of the lateral groove (*see* fig. 1). The central region of the clubbed process is situated immediately posterior to the cuticular ridge. The clubbed process and its base are covered with hydrofuge cuticle secreted by a columnar epithelium with large oval nuclei, while the cavity of these structures is filled with non-cellular ground tissue (fig. 3, *GT*). The clubbed process, though relatively immobile, is capable of a certain degree of rotation in both the transverse and longitudinal planes. Immediately posterior to Hagemann's organ lies the posterior thoracic spiracle (figs. 1 and 2, *PTS*). This consists of a short atrium, closed at its outer end by two spiracular lips, the anterior being the larger. The outer wall of the lateral pouch is composed of two layers of cuticle, the outer layer being thicker than the inner (fig. 4). Each cuticular layer is composed of an epicuticle, a tanned exocuticle and an untanned flexible endocuticle, which stains green with Masson. Between these two cuticular layers are an inner and an outer layer of hypodermis separated by haemocoel (fig. 4, *HM*). The two layers of cuticle are connected by a number of cuticular pillars (fig. 4, *CTP*) which are formed from invaginations of the inner layer of cuticle. Each pillar contains a central core of epicuticle and tanned exocuticle, surrounded by a thin endocuticle and hypodermis. At their outer ends, the cuticular pillars are fused to the endocuticle of the outer layer (fig. 4). These cuticular pillars act as internal braces between the inner and outer cuticular layers. If the outer wall of the lateral pouch were bent outwards, the inner cuticular layer and cuticular columns would be stretched to accommodate this change. Opposite changes would occur if the outer wall of the lateral pouch were bent inwards (*cf.* fig. 5). The presence of an inner core of elastic, non-flexible cuticle in the cuticular pillars inhibits any such pillar movements, and the outer wall of the lateral pouch must, therefore, retain its normal position irrespective of pressure differences between the pouch and the exterior. The inner wall of the lateral pouch is composed mainly of thick hard elastic sclerotin. This means that as the insects descend from the water-surface and the hydrostatic pressure increases, the volume of the lateral pouch remains unchanged. The surfaces of the cuticular ridge, the lining of the lateral pouch and the surface of the thorax bear numerous hair-like setae, which, standing at right angles to the body surface, are responsible for its hydrofuge property.

FUNCTION OF HAGEMANN'S ORGAN

Hagemann's suggestion that the membrane vibrated like an ear drum in response to sound waves is difficult to accept, because the base of the clubbed process must tend to damp vibrations of the membrane. Physical considerations show that the minimum frequency to which the clubbed process can resonate is of the order of 300,000 vibrations per second (*i.e.* a wavelength of four times the length of the clubbed process). In smaller corixid species, the minimum frequencies to which the clubbed process could resonate would exceed 1,000,000 vibrations per second. Such high frequencies rapidly lose their energy on transmission and for that reason their audible range is extremely short. It is, therefore, unlikely that Hagemann's organ has an auditory function.

A second possibility, that the organ is a gravity perceptor, is excluded by the fact that corixids swim and surface normally when the clubbed process is extirpated on one or both sides of the body.

Normally, corixids tend to move down a dorsal light gradient along the habitat bottom into deeper water. The additional hydrostatic pressure reduces the size of the superficial gas stores and a stage is eventually reached when water could enter the spiracles and flood the tracheal system. It is, therefore, essential that corixids should have a suitable organ capable of warning them before tracheal flooding occurs. It is this function which Hagemann's organ performs.

METHOD OF RESPIRATION

When submerged, *Corixa punctata* carries a superficial gas bubble on the ventral body surface and another between the wings and abdominal tergites. Gas is expired mainly through the latero-ventrally placed anterior thoracic spiracles, and then moved backwards over the abdominal ventral surface by the hind legs. A smaller amount of gas is expired from the posterior thoracic spiracles and is moved backwards by the hind legs, under the wings, on to the dorsal surface of the abdomen. The dorso-ventral flattening of the abdomen facilitates gaseous exchange between the superficial abdominal gas stores and the surrounding water. The ventrally placed abdominal spiracles are minute and lead into fine tracheae supplying the gut and gonads. The longitudinal abdominal tracheae are exceptionally fine and the amount of gaseous exchange between the thorax and the abdomen may be regarded as negligible. Air is mainly inspired through the dorsally placed anterior abdominal spiracles, which are situated laterally in arthrodial membrane between the metatergum and first abdominal tergite and also just mesad to the metepimeron. The anterior abdominal spiracle lies in the lateral pocket and is therefore in contact with the dorsal and ventral gas stores (Popham, 1959, 1960).

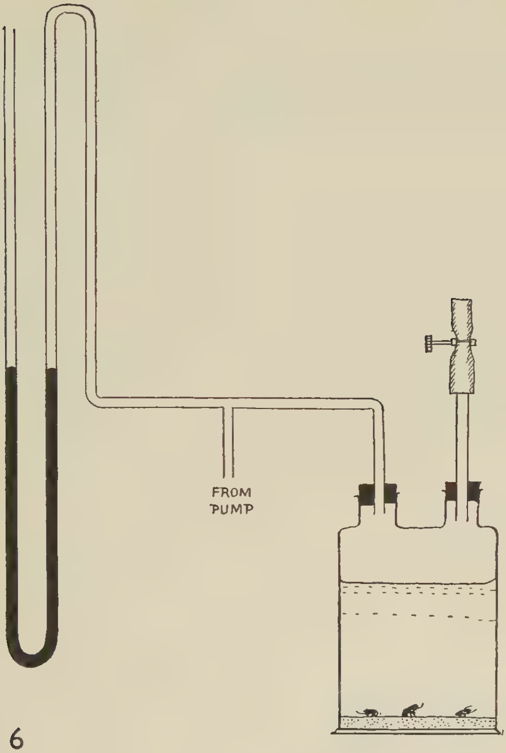
TRACHEAL FLOODING

It would appear that water cannot easily enter the ventral abdominal spiracles on account of their small size, nor can it easily enter the anterior thoracic spiracles, which are used for expiration. Water cannot easily enter the anterior abdominal spiracles, because these are surrounded by sclerites composed of hydrofuge material and the spiracles themselves lie in deep depressions, one on each side of the insect. Water could reach the posterior thoracic spiracles as follows. The lateral groove is normally closed anteriorly by the folded auxillary sclerites of the front wing, dorsally by the hemi-elytron and laterally by the thoracic pleura. This means that water can, therefore, reach Hagemann's organ only by first entering the sub-elytral space and then moving forwards dorsally over the mouth of the lateral groove and pouch. No other method of approach is possible. Water could reach Hagemann's organ in this way during inspiration of gas from the dorsal abdominal gas stores. By lifting the hemi-elytron and slowly lowering the insect into water, with head slightly pointing upwards, the action of water upon Hagemann's organ can be studied, the outer wall of the lateral pouch being removed to facilitate observation.

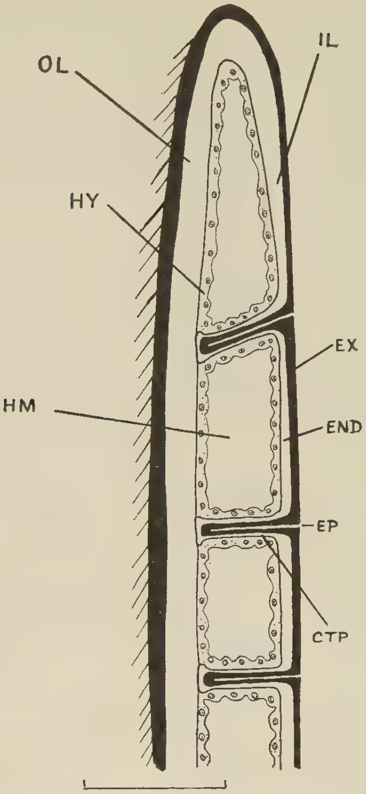
MODE OF ACTION

The hydrofuge incurved lips of the lateral groove prevent water entering the groove itself. As the insect is lowered, water advances along the groove opening towards the anterior end of the lateral pouch. The narrowness of the openings of the groove and pouch, and the position and form of the lips, allow the water to hang as a suspended droplet into the lateral groove. As the water continues to move forwards, it eventually reaches the hydrofuge knob of the clubbed process, which is then pushed forwards until it touches the cuticular ridge, which acts as a stop and inhibits further movement. When the insect is raised, water retreats and the clubbed process returns to its original position, by virtue of the elasticity of the membrane.

Rotation of the clubbed process towards the cuticular ridge causes an increase in the length of the base on the side towards which turning takes place and a reduction in the length of the other. The hump is shaped like a rectangular box, open on its inner side. Being composed of hard elastic cuticle, the hump is better able to maintain its shape than is the base of the clubbed process. This rotation of the clubbed process is, therefore, accompanied by an increase in the tension of the scolophores on the side towards which the clubbed process moves, and a reduction

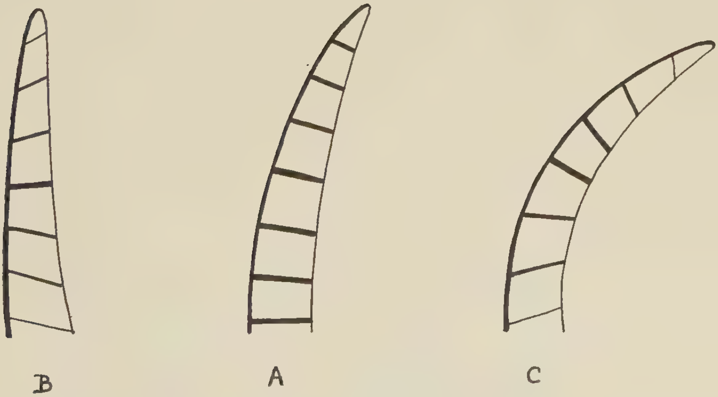


6



4

5



Figs. 4–6.—(4) Transverse section of outer wall of lateral pouch of *Corixa punctata*. (5) Changes in the structure of outer wall of lateral pouch (*A*), if it were bent outwards (*B*), or inwards (*C*), and the cuticular pillars were composed entirely of flexible non-elastic endocuticle. (6) Apparatus used for studying the effects of pressure increases upon corixids.

of the tension of the scolophores on the other. These changes of tension lead to changes in the stimulation of the nerve fibres of the organ.

The organ can be artificially stimulated by fastening the clubbed process to the cuticular ridge by means of molten wax, run on to the clubbed process with a warm needle. Twelve specimens of *Corixa punctata*, with the lateral pouch exposed by lifting one hemielytron and then replacing it, behaved normally when returned to water. The same number of insects, each with the clubbed process of one organ attached to the cuticular ridge, floated horizontally at the surface and could not be induced to swim to the bottom until the clubbed process and cuticular ridge separated. Insects, with water artificially introduced into the lateral pouch, behaved in a similar manner. As these operations do not interfere with the normal methods of respiration, it would appear that stimulation of Hagemann's organ causes surfacing.

If the insect is held horizontally on its side, and lowered into water with an air bubble over Hagemann's organ and the wall of the lateral pouch removed to facilitate observation, it will be seen that, as the insect is lowered into the water and the hydrostatic pressure increases, the membrane becomes increasingly concave and the clubbed process rotates dorso-laterally away from the insect; movement is in the opposite direction as the insect is raised and the pressure reduced. A similar change must take place when the spiracles open and the pressures between the tracheal system and the exterior are equalised. These changes in the position of the clubbed process cause modifications of scolophore tension and stimulation of the nerve fibres. It is possible, therefore, that Hagemann's organ can also be used to detect slight changes of pressure. In this connection, it is interesting to note that in the dark corixids tend to aggregate in the deepest parts of shallow bodies of water or of experimental tanks.

By means of an air pump connected to a manometer and a flask containing ten specimens of *Corixa punctata* (fig. 6), the pressure on the submerged corixids was gradually increased and measured. As the pressure rose, the dorsal and ventral gas stores contracted and gas was expired from the thoracic spiracles in increased quantities. This gas was then moved backwards on to the abdominal surface by the hind legs. When the pressure reached values normally to be encountered at depths ranging from 10 to 25 feet of water (average of 40 surfacings), the insects first became increasingly active and then surfaced. Insects with the pronotum fixed with wax against the wing bases to hold the wings against the dorsal body surface and to inhibit (at least partially) the entry of water into the sub-hemielytral space, failed to surface or show any increase of activity over this range of pressure increases.

The form of the lateral pouch and groove calls for special comment. There can be little doubt that the pleural walls protect Hagemann's organ, but that does not account for the exceptionally large size of the lateral pouch which is possibly used as a water trap. In the Corixidae, where the gas stores are moved over the body surface during respiration, any organ which is to perceive a reduction in the size of the gas stores with increased hydrostatic pressure can only function effectively if it is situated in an air pocket, the volume of which remains constant. It is this function which the lateral pouch performs, the cuticular pillars described above inhibiting movement of the outer wall and thus maintaining a constant pouch volume.

A membrane with attached scolophores occurs in *Ilyocoris* and *Notonecta*, in a homologous position to Hagemann's organ in *Corixa*. Although these organs may have an auditory function, it is also possible that they are used to perceive hydrostatic pressure changes, but this is a matter for investigation.

CONCLUSIONS

The facts given above are consistent with the hypothesis that *Corixa punctata* surfaces because of stimulation of Hagemann's organ, water entering the sub-hemielytral space, rotating the clubbed process and thus stimulating the scolophores. Such stimulation normally occurs when the insects descend to a depth exceeding 10 feet of water.

Acknowledgments

I wish to thank Professor H. Graham Cannon, F.R.S., in whose department this work was done, Miss D. E. Ashhurst for her help and advice in the preparation of the celloidin sections and Miss Gorna, who has kindly typed the script.

References

Ege, R., 1915, On the respiratory function of the air stores carried by some aquatic insects (Corixidae, Dytiscidae and *Notonecta*). *Z. allg. Physiol.* **17** : 81–125.
Hagemann, J., 1910, Beiträge zur Kenntnis von *Corixa. Zool. Jahrb. Anat.* **30** : 373–426.
Popham, E. J., 1959, Respiration of Corixidae (Hemiptera-Heteroptera) *Nature, Lond.* **183** : 194.
—— 1960, On the respiration of aquatic Hemiptera Heteroptera with special reference to the Corixidae. *Proc. zool. Soc. Lond.* **135** : 209–242.

Explanation of Figure Lettering

*B*1, flask shaped structure forming upper part of " base ".
*B*2, flask shaped structure forming lower part of " base ".
CP, clubbed process of Hagemann's organ.
CR, cuticular ridge.
CTP, cuticular pillars.
DG, dorsal ganglion.
END, endocuticle.
EP, epicuticle.
EX, exocuticle.
GT, ground tissue.
H, hump for insertion of scolophores.
HM, haemocoel.
HY, hypodermis.
IL, inner layer of cuticle.
OL, outer layer of cuticle.
LG, lateral groove.
LP, lateral pouch.
LTT, lateral tracheal trunk.
M, membrane of Hagemann's organ.
N, nerve.
PTS, posterior thoracic spiracle.
SC, scolophores.

THE FUNCTION OF THE STERNAL SPATULA IN GALL MIDGES[1]

By D. L. Milne
(*Rothamsted Experimental Station, Harpenden, Herts.*)[2]

Introduction

Many functions have been assigned to the sternal spatula, such as its use as a digger or scraper of plant tissue to get food, and to reverse the larval position in the cocoon (Metcalfe, 1933) ; for clearing a space (by resin-inhabiting midges), for leaping, for preparing an emergence hole for the imago of species inhabiting woody galls, and for moving through the soil (Kieffer (1900) quoting Giard, 1894, *unpublished*).

Felt (1925) found small wood fibres in galleries made by stem-inhabiting species and suggested that *Monardia lignivora* Felt, *Neolasioptera hibisci* Felt and *Lasioptera galeopsidis* Felt use the sternal spatula for boring. Eckel (*in* Felt, 1925) found that, where *Retinodiplosis resinicola* Osten-Sacken is present, the soft resin contains numerous microscopic splinters, presumably produced by the action of the sternal spatula. Sen (1939) concluded that *Rhabdophaga saliciperda* Dufour, a species inhabiting woody galls of willow, uses the spatula as a perforator when the larva travels towards the outer bark for pupation.

In *Dasyneura tetensi* (Rübsaamen) the sternal spatula is worn down when the larva burrows through the soil and makes a cocoon (Pitcher, 1957). Pitcher noted more wear in a sand and carborundum mixture than in other media. In *D. tetensi* the main function of the spatula appears to be for tunnelling in the soil and excavating a pupal cell.

The Present Investigation

Dasyneura leguminicola Lintner, *D. gentneri* Pritchard, *Tricholaba barnesi* Milne and *Phaenobremia aphidivora* Rübsaamen were studied to see whether the sternal spatula became worn, and to find out how it is used. The larvae of the first three species feed on the ovaries of clover, flowers dropping to the soil when they are fully fed, to spin their cocoons. Larvae of *P. aphidivora* are predatory on aphids infesting the stems and leaves of clover plants, but they also drop to the soil when fully fed.

Material and Methods

Mature larvae of *D. leguminicola*, *D. gentneri*, *T. barnesi* and *P. aphidivora* were collected. Some with unworn spatulae were preserved in 70 per cent. alcohol. An equal number was kept alive and confined to observation tubes (fig. 1), containing white sand, globular perspex, or cotton wool. These larvae were then watched through the microscope (magnification 100 diameters) as they moved through the soil, sand or other media, cleared a space for cocoon spinning, and formed the cocoon. Some larvae were removed when cocoon spinning was complete, and others only when the sternal spatula was shed with the last larval skin at pupation. Both these groups were preserved in 70 per cent. alcohol and labelled *worn*.

All larvae were mounted : some spatulae were detached to ensure a flat mount. Specimens from both *worn* and *unworn* groups were then compared.

Observations and Results

Dasyneura leguminicola was studied in the three media, and maps were made, showing the depths of the cocoons, by enclosing the observation tube in a cylinder of

---

[1] This work forms part of a study submitted to London University for the Ph.D. degree.

[2] Now at Central Tobacco Research Institute, Rustenburg, South Africa.

PROC. R. ENT. SOC. LOND. (A) 36. PTS. 7–9. SEPTEMBER, 1961.

cellophane paper and inking in the positions on the paper, which could then be opened out and the positions traced off. Most of the larvae settled in the upper 2 cms. of sand but in cotton wool they went deeper. This suggests that in heavy clay the larvae may not go as deep as they will in loam.

Two distinct methods (*A* and *B*) of using the sternal spatula were observed. The larva may first appear to investigate an obstacle with the palps, then to thrust forward so that the sternal spatula comes in contact with the obstacle, and finally to arch backwards, thereby completing a scooping action (fig. 3); this was observed from lateral and ventral positions: or, after an investigation with the palps, the larva retracts the head and supernumary segment so that the lobes of the spatula are foremost, and then thrusts forward using the sternal spatula as the foremost point of contact; this method was observed from the ventral, lateral and dorsal positions. Felt (1925), writing about the galleries of *Lasioptera galeopsidis* states, " we have repeatedly seen larvae with the head and body segments retracted so that the anterior portion of the breastbone projected forward like the point of a chisel ", and it seems probable that the spatula was serving a similar function in *D. leguminicola*. Both methods were observed at two different stages—as an aid to burrowing when the larva enters soil, and when clearing a space before cocoon-spinning. Once cocoon spinning has begun the spatula is no longer used.

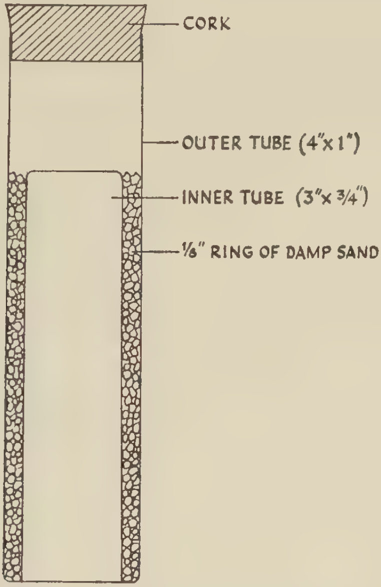


Fig. 1.—Section of observation tube.

There were different degrees of wear in different media, as reported by Pitcher (1957); cotton wool produced least and sand most (fig. 4); sometimes, in sand, nearly all the protruding part of the spatula was worn away. Parasitism of the larvae seemed to have no effect on the degree of wear. When the cocoon was complete, the larva continued to move round inside taking a variety of positions throughout each day, but this caused no obvious additional wear. Very little wear was observed in larvae which moved only on the surface.

Results with *Dasyneura gentneri* were similar. The sternal spatula is considerably smaller than that of *D. leguminicola* and the lobes are less pointed so that differences are more difficult to interpret, but very obvious signs of wear could still be detected,

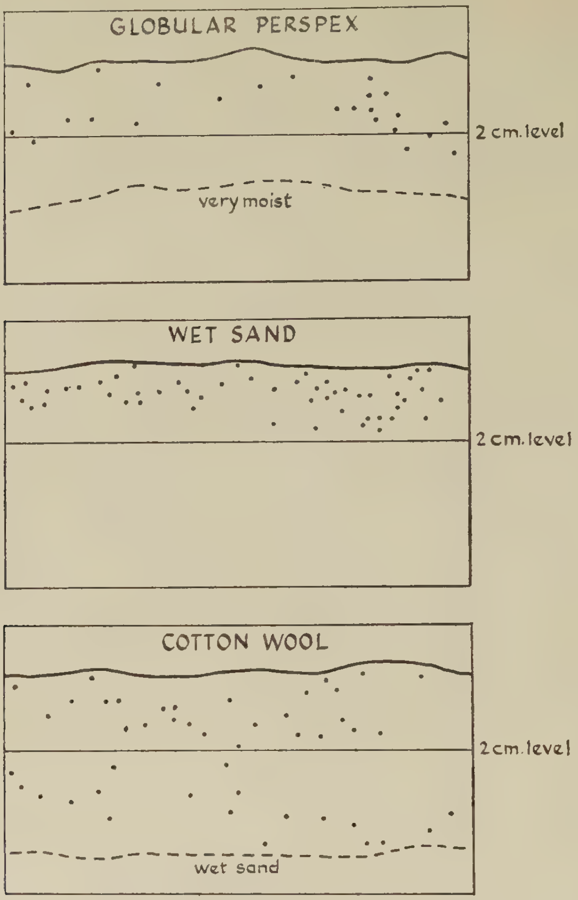


FIG. 2.—Depths of larvae of *D. leguminicola* in observation tubes containing three different media.

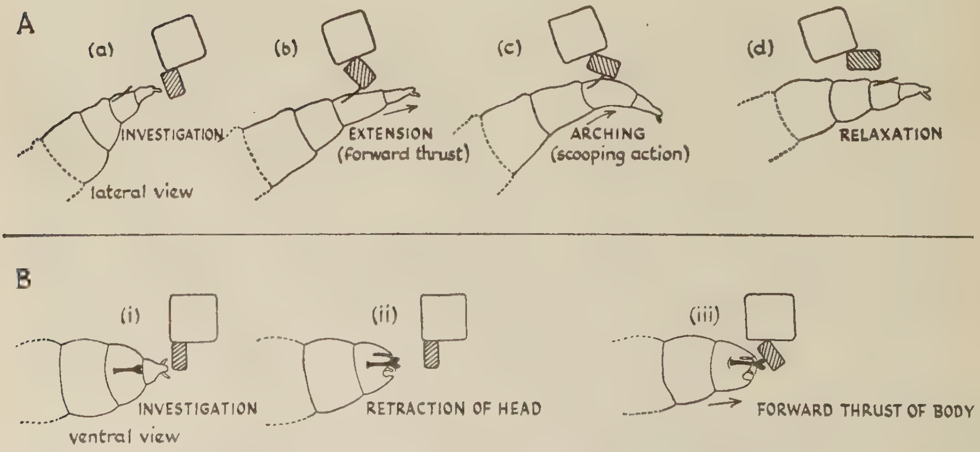


FIG. 3.—Two modes of use of the sternal spatula employed by Cecidomyid larvae : (*A*) a scooping motion ; (*B*) a forward thrusting motion.

the lobes of specimens spinning cocoons in observation tubes containing wet sand being almost completely worn away, or bearing a nearly straight edge anteriorly (fig. 4). *D. gentneri* was observed removing obstacles on several occasions, both on entering the medium and in clearing a cell for cocoon-spinning.

Tricholaba barnesi can spring by forming a hoop and then rapidly releasing its " hold ", in a similar way to *Contarinia tritici* Kirby (Barnes, 1956). A remarkable variety of methods of forming the " loop " prior to springing was observed : (*a*) the head may fit between the last two segments of the abdomen ventrally, (*b*) the anal segment may be wedged between any two thoracic segments ventrally, or (*c*) the head and thorax may be bent backwards, the anal segments resting between the thoracic segments dorsally. Although on occasions in position (*b*) the anal segments were in contact with the sternal spatula, the spatula was not seen to project noticeably and, in fact, the attitude of the larva would tend to keep it close to the epidermis. Therefore, in this case as well as on the many occasions when methods (*a*) or (*c*) were used, the spatula was not used as an aid to jumping. The anal projections on the larva appear to help in obtaining a firm " hold " prior to springing and fit closely between the segments against which they are braced. On entering the sand these larvae were observed to use the sternal spatula in both the ways shown in figure 3—in burrowing through the sand and in clearing a site for cocoon spinning. The comparison of worn and unworn spatulae (fig. 4) shows that very marked wear occurs during this burrowing. The wear in some cases is probably more marked than it would be under most natural soil conditions.

In *Phaenobremia aphidivora* the larvae are free living during all instars but the sternal spatula is present only during the last two, its stem being more distinctly sclerotised in the final instar. After entry into the soil the spatula was used mainly in clearing a space for cocoon spinning, using method *A*. Spatulae of larvae removed from cocoons again were very worn, the indentation between the lobes being almost indiscernible in some (fig. 4). The larva of this species also moves round very frequently in the cocoon, but this movement causes no obvious additional wear.

The predator *Lestodiplosis trifolii* has no sternal spatula and does not spin a cocoon or clear a space in the soil before pupation. In the genus *Miastor*, paedogenesis occurs in some larvae, ; those that reproduce paedogenetically have no spatula but in those that pupate and undergo normal development to the imago the spatula is developed prior to pupation. Possibly, therefore, this species uses the spatula to hollow out a pupal chamber.

CONCLUSIONS

It seems unlikely that *D. leguminicola*, *D. gentneri* and *T. barnesi* use the spatula to abrade plant tissues and get food, for it is well-developed only in the later instars and no noticeable wear could be detected in larvae that were examined immediately after they had left the plants. Larvae of *P. aphidivora* feeding on aphids were not observed to use the spatula to damage their hosts in any way. The spatula is not of great importance in the leaping movements of *T. barnesi*, as various springing methods were observed in which the spatula did not come in contact with any other part of the body. No signs of the preparation of a pre-emergence cap in the cocoon were detected in any of these species. The spatula is not used to reverse the larval position in the cocoon in these species ; pupae of *D. leguminicola* and *T. barnesi* can reverse their positions in the cocoon at quite an early stage of development, although this was uncommon.

In these four species, and possibly in many others which pupate in the soil, the main function of the spatula is to excavate a pupal chamber in the soil, and it may also be used in a very similar manner in species inhabiting woody tissues.

The spatula may become worn and identification of larvae removed from the soil on the form of the spatula alone may be difficult.

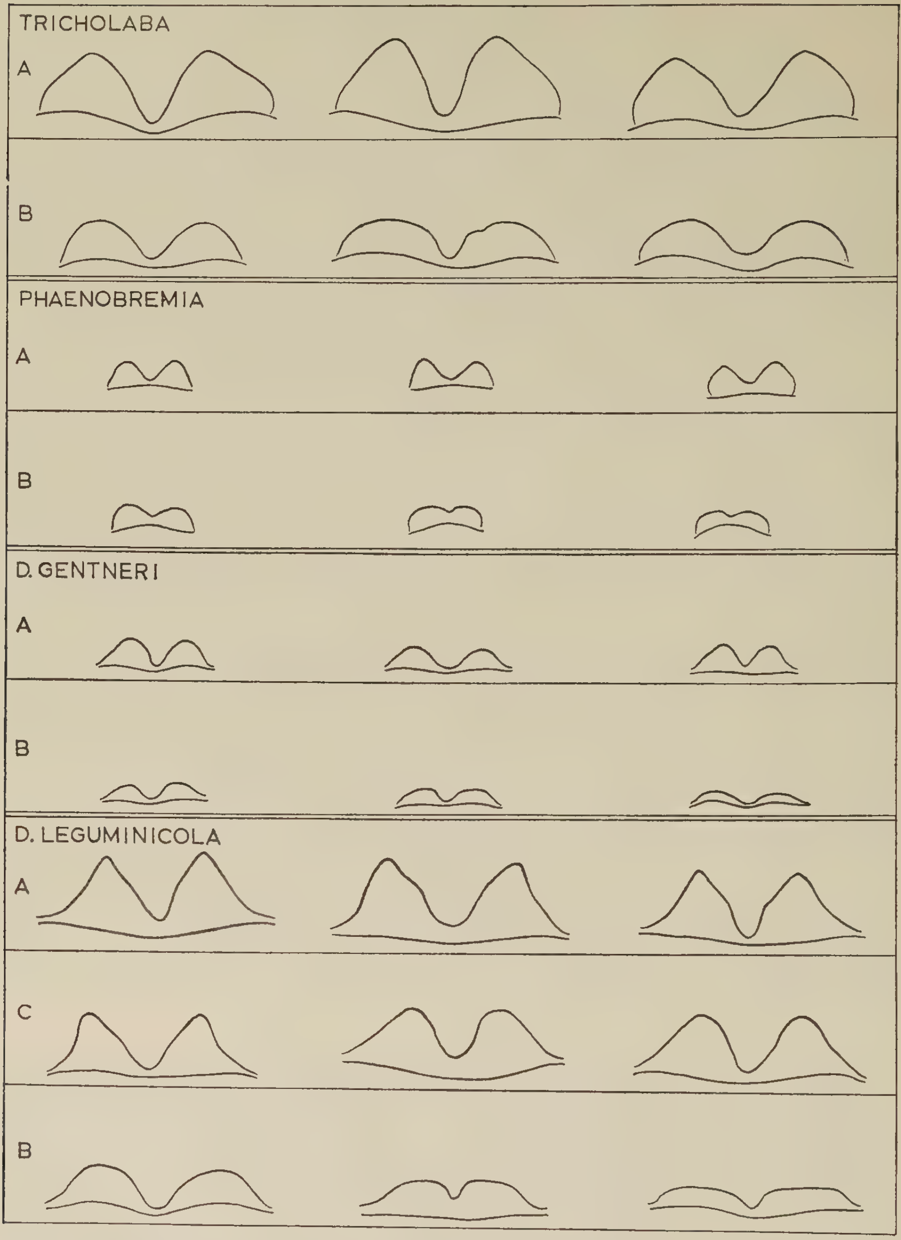


FIG. 4.—Lobes of the sternal spatula of larvae belonging to three genera, showing the wearing that occurs during subsoil activities: (*A*) unworn spatulae from larvae killed and mounted before they have entered the soil; (*B*) spatulae worn down in sand (in observation tubes); (*C*) spatulae slightly worn in cotton wool (in observation tubes).

ACKNOWLEDGMENTS

The author wishes to express his indebtedness to the late Dr. H. F. Barnes for his help and constructive criticism during this work, and also to thank Dr. K. Mellanby for allowing him the facilities of the Rothamsted Entomology Department where the work was carried out.

References

Barnes, H. F., 1956, *Gall Midges of Economic Importance. Vol. VII. Gall Midges of Cereal Crops.* London, 261 pp.

Felt, E. P., 1925, Key to Gall Midges (A Résumé of Studies I–VII, Itonididae). *Bull. N. Y. St. Mus.* **257** : 239 pp.

Kieffer, J. J., 1900–1, Monographie des Cécidomyidae d'Europe et d'Algérie. *Ann. Soc. ent. Fr.* **69** (1900) : 181–472.

Metcalfe, Margot E., 1933, The Morphology and Anatomy of the larva of *Dasyneura leguminicola* Lint. (Diptera). *Proc. zool. Soc. Lond.* **1933** : 119–30.

Pitcher, R. S., 1957, The abrasion of the sternal spatula of the larva of *Dasyneura tetensi* (Rübs.) during the post-feeding phase. *Proc. R. ent. Soc. Lond.* (A) **32** : 83–89.

Réaumur, R. A. F. de, 1736–40, *Mémoires pour servir à l'histoire des Insectes,* II–V. Paris. (Quoted from Pitcher, R. S., 1957).

Sen, P., 1939, On the function and development of the sternal spatula in the Cecidomyidae or Gall Midges as exemplified by *Rh. saliciperda* Duf. *J. Morph.* **65** : 1–15.

BOOK NOTICE

Annual Review of Entomology. Vol. 6. Edited by E. A. STEINHAUS and R. F. SMITH. 8vo. Palo Alto (Annual Reviews, Inc.), 1961. Pp. vii, 470, text illust. $7.50.

This is the most recent volume of the series and contains the following papers :

Darwin's contributions to entomology, J. E. Remington and C. L. Remington.
Insect nutrition, H. L. House.
Nutritional factors in insect resistance to chemicals, H. T. Gordon.
Principles of insect cold-hardiness, R. W. Salt.
The biochemistry of insect hemolymph, G. R. Wyatt.
The role of mitochondria in respiratory metabolism of flight muscle, B. Sacktor.
Diurnal rhythms, J. E. Harker.
The theoretical and practical study of natural insect populations, O. W. Richards.
Principles of insect predation, C. S. Holling.
Biological control of pest insects in Europe, J. M. Franz.
Sampling crop pests and their hosts, A. H. Strickland.
Biology of chiggers, M. Sasa.
The phenomenon of industrial melanism in Lepidoptera, H. B. D. Kettlewell.
A review of the phylogeny of mites, T. A. Woolley.
Palaeoentomology, O. Martynova.
The analysis of insect embryogenesis, S. J. Counce.
The chemistry of organic insecticides, T. R. Fukuto.
Mode of action of insecticides, C. C. Roan and T. L. Hopkins.
Ecological aspects of plant virus transmissions, W. Carter.
Mechanism of transmission of viruses by mosquitoes, R. W. Chamberlain and W. D. Sudia.
Arthropod vectors as reservoirs of microbial disease agents, C. P. Philip and W. Burgdorfer.
Transmission of filarioid nematodes, F. Hawking and M. Worms.

It has, in addition to its own author and subject indices, cumulative indices of chapter titles and authors contributing to volumes 2 to 6.

PUBLICATIONS

The principal Publications of the Royal Entomological Society are *Transactions* and *Proceedings.*

The **Transactions** form an annual volume, each paper in the volume being issued as a separate part. The parts are issued irregularly throughout the year.

The **Proceedings** are issued in three series :

Series A.	**General Entomology**
Series B.	**Taxonomy**
Series C.	**Journal of Meetings**

Series A and B are issued in twelve parts, forming an annual volume of approximately 240 pages each.

The following information is supplied for the guidance of authors wishing to submit papers for publication in any of the Society's journals.

TRANSACTIONS

Papers offered for publication in the *Transactions* are considered by the Publication Committee of the Society which meets usually in the months of May and November. In order that papers may be considered at these meetings it is necessary for the manuscript and drawings for illustrations to be in the hands of the Registrar as early as possible. Papers received *after* 1st April and 1st October cannot be considered at the meeting immediately following.

The Society is prepared to undertake the provision of a reasonable number of figures, in line or half-tone. Colour work is accepted only by special arrangement.

Papers of less than eight printed pages (approximately 5,000 words) will not normally be accepted for the *Transactions* and papers by authors who are not Fellows of the Society must be communicated by a Fellow.

PROCEEDINGS SERIES A AND SERIES B

Papers submitted for publication in either *Series A* or *Series B* of the *Proceedings* are considered by the Editor and may be submitted at any time. Papers by authors who are not Fellows of the Society may be accepted if they are communicated by a Fellow.

Line blocks will be provided by the Society. Half-tone and colour work are accepted only by special arrangement and the author may be required to pay for the blocks.

PROCEEDINGS SERIES C

Series C is issued before every General Meeting. It contains abstracts of communications to be made, together with the titles of papers accepted for publication in the *Transactions.*

The annual subscription to *Series A*, *General Entomology*, is £2 8*s.* 0*d.* ; *Series B*, *Taxonomy*, £2 8*s.* 0*d.* ; and *Series C*, *Journal of Meetings*, £1 0*s.* 0*d.*

As from January, 1936, the journal *Stylops* is continued as *Proceedings Series B*, *Taxonomy.* Copies of volumes 1–4 are available at £1 16*s.* 0*d.* each, post free.

GENERAL

The original drawings for all figures must be supplied by authors and must be drawn to a scale which will permit of their reduction, singly or after grouping, to an area of dimensions not exceeding 7 by 5 in.

A uniform method is adopted for the citation of bibliographical references in the Society's publications as follows :

Smith, A., 1935, New species of Coccidae. *Proc. R. ent. Soc. Lond.* (B) **6** : 301–6, pl. 1.

—— 1936, New species of Coccidae. *Trans. R. ent. Soc. Lond.* **84** : 901–36.

Titles of periodicals cited are to be abbreviated in the manner indicated in the *World List of Scientific Periodicals, 3rd edition*, 1952.

Authors are entitled to receive 25 copies of their papers free of charge and may purchase additional copies provided that request be made before publication.

Papers offered for publication should be sent to the Registrar, Royal Entomological Society of London, at 41, *Queen's Gate, London, S.W.*7, and must be typewritten on one side of the paper only, with double spacing. **All papers in the Transactions must be provided with a summary.**

All the Society's publications are copyright.

MEETINGS

TO BE HELD IN THE SOCIETY'S ROOMS
41, Queen's Gate, S.W.7

1961
Wednesday, November 1
„ December 6

1962
Wednesday, January 17

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

The Fellowship and Fees

Fellows pay an Admission Fee of £2 2*s*. The Annual Contribution, £3 3*s*., is due on the first day of January in each year, and is payable in advance. Fellows under the age of 25 years on the date of election are exempt from the payment of the Entrance Fee.

Fees should be paid to the Registrar, at 41, Queen's Gate, S.W.7.

Fellows desiring to pay their Annual Contribution through their bankers may obtain an official form of bankers' order by applying to the Registrar.

Fellows whose Contributions for the current year have been paid are entitled to receive the *Transactions* and *Proceedings* of the Society free of charge. Further copies may be purchased at reduced prices by applying to the Registrar.

Forms of application for Fellowship, copies of the Bye-Laws and the List of Fellows may be obtained from the Registrar.

Meetings and Exhibitions

Fellows and others wishing to make a communication to a General Meeting of the Society are requested to send in their names, the title of their exhibit, and a short abstract of their remarks, to the Hon. Secretary fourteen days before the meeting at which it is proposed to make the communication. Should it be desirable to publish a fuller account of the communication the manuscript may be submitted for publication in *Proceedings Series A* or *Series B*.

Fellows resident abroad, or otherwise unable to attend meetings, are reminded that notes or observations sent to the Hon. Secretary may be communicated to a General Meeting on their behalf.

PRINTED FOR THE SOCIETY BY ADLARD AND SON, LTD., BARTHOLOMEW PRESS, DORKING.